Restoration ecology of the Seychelles giant millipede

by

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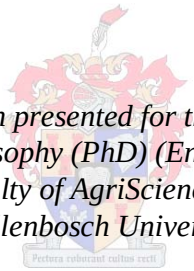

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Declaration

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Abstract

The loss and degradation of habitat is recognised as the greatest threat to invertebrate biodiversity. Restoration practices have the potential to reduce these impacts. The Seychelles giant millipede (SGM), *Sechelleptus seychellarum*, is a threatened and functionally important macro-detritivore endemic to the Seychelles granitic islands. The broad objective of this dissertation was to investigate selected aspects of the restoration ecology of the SGM, with the intention of making practical restoration recommendations that can be used to assist in the conservation of this species. This study was carried out on Cousine Island, Seychelles between 1998 and 2009, in the context of the large-scale plant community restoration that has taken place on the island. Large fluctuations in millipede population densities were found between 1998 and 2009. In 2002, 2003, 2005 and 2007 millipede densities were low, while densities were high in 1998 and 2009. Although the SGM is active all year round, its surface activity was positively correlated with rainfall, with density high during the high rainfall period (i.e. October – April) and low during the low rainfall period (i.e. May – September). Female:male:juvenile ratios were ~ 3:1:1. The implications are that translocations should preferably be done in years of high millipede densities and during the wet season. Alien coconut trees did not affect SGM density, but negatively affected its foraging behaviour, whereas bamboo stands negatively affected both its density and foraging behaviour. The SGM showed feeding preferences for *Pisonia grandis* and *Ficus* sp. leaf litter types. Alien bamboo and coconut pose a varied threat to the SGM, and their removal and replacement by indigenous forest species (e.g. *P. grandis* and *Ficus* sp.) should form part of an island's restoration programme. SGM density was an order of magnitude lower in the restored area compared to the natural forest. In contrast, SGM physical condition improved significantly in the restored area, as vegetation structure increased. Furthermore, SGM behaviour in the restored area switched from a predominantly walking to a predominantly feeding behaviour over the study period, resulting in the forest restoration programme on Cousine increasing the foraging area of the SGM by 43%. SGM spatial density did not significantly correlate with edaphic and litter properties, but did positively correlate with the toposcape (i.e. elevation and granitic rock cover). Granite rock crevices in forest covered areas were important diurnal refuges for the SGM, as microclimate conditions in non-forest covered rock refuges were unsuitable. SGM physical condition was significantly lower in non-shaded crevices compared to those shaded by forest. Low granite rock cover in the restored forest limited the SGM colonisation of this area in large numbers, despite canopy cover in the restored forest being comparable with that in the reference natural forest. As most restoration practices are primarily vegetation-based, this study demonstrates that such an approach can be inadequate for restoring habitat for target invertebrates, as many species' habitat requirements extend beyond that of vegetation. For the SGM, selecting restoration sites that already have abundant rock cover would be the most practical way to increase SGM habitat through forest restoration practices. Taking into consideration the habitat requirements of target invertebrates can help in setting or redirecting restoration goals and thus enhance the conservation value of such practices.

Opsomming

Die verlies en agteruitgang van habitat word alom beskou as die grootste bedreiging var die biodiversiteit van ongewerweldes. Herstellingspraktyke kan hierdie agteruitgang verminder of stop. Die Seychelle Reuse Duisendpoot (SGM), *Sechelleptus seychellarum*, is 'n bedreigde en funksioneel belangrike makro-detritusvoeder wat endemies is aan die Seychelle graniet-eilande. Die breë doelstelling van hierdie verhandeling is die doen van navorsing om praktiese aanbevelings te kan maak om die habitat van die SGM tot so ‘n mate te herstel dat die spesie kan bly voortbestaan. Hierdie studie is tussen 1998 en 2009 uitgevoer op Cousine Island, Seychelles, nadat ‘n grootskaalse herstellingsfase van die plantgemeenskap plaasgevind het. Groot skommelings in duisendpootgetalle is waargeneem tussen 1998 en 2009, *viz.* duisendpootgetalle was laag in 2002, 2003, 2005 en 2007, terwyl dit hoog was in 1998 en 2009. Alhoewel die SGM gedurende die hele jaar aktief is, is hulle tog in groter getalle aanwesig in die tydperke met hoë reënval (Oktober-April) en laag in die droë tydperk (Mei-September). Die verhouding van wyfies, mannetjies en onvolwassenes was deurgaans ~ 3:1:1. Dit bring mee dat hervestiging van SGM verkieslik gedoen moet word wanneer hul populasies hoog is en dan ook in die nat seisoen. Uitheemse klapperbome het geen invloed op SGM getalle gehad nie, alhoewel hul voedingsgedrag negatief beïnvloed is deur dié bome. Bamboesbosse darenteen, beïnvloed beide populasiedigtheid en voedingsgedrag van SGM negatief. Verder is daar gevind dat *Pisonia grandis* en *Ficus* sp. blaardetritus voorkeurvoedsel vir SGM is. Die verwydering van die uitheemse bamboes en klapperbome en vervanging daarvan met inheemse woudspesies (*P. grandis* en *Ficus* sp.) moet dus deel vorm van die eiland se herstelprogram om sodoende die SGM te bevoordeel. Die SGM-bevolkingsdigtheid was 'n grootte-orde laer in die herstelde gebied in vergelyking met die natuurlike bos, maar hul fisiese toestand het aansienlik verbeter in die herstelde gebied, waarskynlik omdat die plantegroei as geheel verbeter het. Verder het die SGM se gedrag gedurende die studietydperk in die herstelde area oorgegaan vanaf ‘n oorwegend loopgedrag om na kos te soek, na ‘n oorwegend voedende gedrag. Die vervanging van uitheemse- met inheemse boomspesies op Cousine Island het dus die voedingsarea van SGM met tot 43% verhoog. Die ruimtelike SGM populasiedigtheid is nie beduidend beïnvloed deur blaardetritus nie, maar is wel positief beïnvloed deur die topografie (hoogte en granietbedekking). Bebosde graniet rotsskeure bied belangrike toevlugsoorde vir SGM gedurende die dag, terwyl die mikroklimaat wat deur onbebosde rotsskeure veroorsaak word, totaal ongeskik is vir SGM. Die fisiese toestand van SGM was ook aansienlik swakker in die nie bebosde rotsskeure teenoor dié van die bebosde areas. In herstelde bos met min granietskuiling was die herkolonisering van SGM ook getalsgewys laer alhoewel die bosbedekking vergelykbaar was met dié van die inheemse bos. Dit bewys dus dat herstellingspraktyke wat hoofsaaklik plantegroei teiken, nie altyd die teikenspesie bevoordeel nie, maar dat ‘n meer holistiese benadering wat alle habitatvoorkeure in ag neem, toegepas moet word. Om SGM te bevoordeel moet herstel areas vir herbebossing dus gekies word waar daar reeds genoegsame granietskuiling is. Deur die habitatvereistes van ongewerwelde teikenspesies in ag te neem kan die herstellingspraktyke meer oordeelkundig ingestel word en sodoende kan die bewaringswaarde van sulke praktyke verbeter word.

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Journal publications and disclaimer

Chapters 2 to 5 from this dissertation have been published in scientific journals (copyright of these papers is owned by the respective journals). Each paper is written in the format of the specific journal with minor modifications for dissertation format consistency. The published articles are as follows:

Chapter 2: Lawrence, J.M., Samways M.J., Kelly, J.A. and Henwood, J. 2013. Population dynamics of a threatened giant millipede: implications for restoration. Invertebrate Biology 132(1):46-51.

Chapter 3: Lawrence, J.M., Samways, M.J., Kelly, J.A. and Henwood, J. 2013. A behavioural ecology approach to assessing the effect of alien vegetation on a threatened giant millipede. Journal of Insect Behaviour 26(3):428-439.

Chapter 4: Lawrence, J.M., Samways, M.J., Kelly, J.A. and Henwood, J. 2013. Response of a threatened giant millipede to forest restoration. Journal of Insect Conservation 17(2):367-373.

Chapter 5: Lawrence, J.M., Samways, M.J., Kelly, J.A. and Henwood, J. 2013. Beyond vegetation-based habitat restoration for a threatened giant Spirostreptid millipede. Journal of Insect Conservation 17(3):557-564.

Disclaimer:

Please note that as Chapters 2-5 of this dissertation were published as stand alone scientific papers, there is some repetition in the various sections. The abstract was translated into Afrikaans by Dr. Antoinette Swart.

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CHAPTER 1

General introduction

1.1. Background

Tropical islands worldwide are losing indigenous biodiversity at an increasing rate from various, often synergistic, impacts (Primack 2006). The impacts caused by habitat loss (Samways 2005), in combination with other threats, in particular invasive alien species (Davies 2009), may lead to a 'meltdown' in the ecological character of the island (O'Dowd et al. 2003). This is particularly relevant for Seychelles invertebrate biodiversity, with its high levels of endemism (Gerlach 2008a), and with the islands having undergone widespread historical anthropogenic degradation (Stoddart 1984; Küffer 2006).

Restoration practices can potentially reduce these threats (e.g. Kawakami and Okochi 2010; Lamb 2011). It has been predicted that ecological restoration will come to dominate future conservation efforts (Young 2000). Restoration ecology, defined by the Society for Ecological Restoration (SER) as "the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed", has experienced rapid growth over the last several decades. However, the success of these efforts it not always guaranteed, and it was frequently assumed that animals would colonise restored sites from surrounding areas as the succession of vegetation proceeded (Majer 2009). Many studies that have addressed invertebrate colonisation of restored sites often reveal poorer diversity and lower abundance in these restoring/restored sites (e.g. Armitage and Fong 2004; Miller and Hobbs 2007).

The term habitat restoration is frequently used in the literature to cover the general topic of restoring ecosystems for the specific purpose of providing habitat either for individual species or for an entire suite of species likely to be found in the area, and more broadly to represent the restoration of native plant communities (Miller and Hobbs 2007). Habitat is most frequently, and incorrectly treated as being synonymous with a particular vegetation, or more specifically, biotope type (Webb 1993). A biotope is understood to mean a region (an area for example: woodland, tropical forest, heath, cliff) that is distinguished by particular environmental conditions and will therefore tend to contain a characteristic assemblage of species (Calow 1999). Historically, most restoration projects have been vegetation-based (Young 2000) and therefore only restore a specific biotope. Habitat is a species-specific concept (Hall et al. 1997) and is far better understood in terms of a species resource requirements (Dennis 2010). A biotope (e.g. vegetation-based for most restoration projects) approach to habitat restoration is of limited use, and

will only result in a haphazard colonisation of the desired fauna (Morrison 2002; 2009), principally common eurytopic species (Samways 1994). This distinction between biotope and habitat can have important implications for threatened animal conservation, where restoration practices have been identified as a potentially viable management approach. The specialised needs of many threatened invertebrates are only now starting to be understood, and many aspects of practical habitat enhancement are based on generalised principles, rather than on detailed direct autecological knowledge of the species involved (New 2009).

Invertebrates, especially ground dwelling taxa, are now playing a greater role in assessing the success of restoration practices, by comparison of their diversities in restored sites to those in natural reference sites (e.g. Andersen 1993; Williams 1993; Bisevac and Majer 1999; Andersen and Sparling 1997; Tajovsky 2001; Longcore 2003; Ruiz-Jaen and Aide 2005). Species composition and richness estimates, however, provide only part of the picture (Lindell 2008), and are generally only useful in assessing the success of a restoration project. By focussing on the restoration of a target species, greater insight into the actual response (i.e. both ecologically and behaviourally) of animals to these projects will be gained, which can have important implications for directing and setting of restoration goals.

As a result, this dissertation aims to investigate selected aspects of the restoration ecology of the Seychelles giant millipede (SGM), *Sechelleptus seychellarum* (Desjardins 1834) (Diplopoda: Spirostreptida: Spirostreptidae) in order to make practical restoration recommendations that can be used to assist in the conservation of this species. This study was carried out on Cousine Island, Seychelles, as this island has both pristine indigenous and restored forest biotopes (Samways et al. 2010a) making it ideal for such a study. In order to achieve this objective the following aspects were investigated:

1) Understanding the basic ecology (i.e. population density dynamics) of the SGM in its undisturbed indigenous forest habitat;

2) Identifying the potential threats (i.e. alien vegetation) the SGM faces.

3) Assessing whether vegetation-based restoration practices can reduce these potential threats.

4) Identifying ways in which the restoration programme can be directed or re-directed in order to create suitable habitat for the SGM.

These four aspects will be further expanded upon in section 1.6..

1.2. Choosing target species for restoration

In general, target species fall into three broad categories:

1) Surrogate species. Surrogate species include indicator, umbrella, keystone and flagship species. While surrogate species are often politically and practically useful in helping to stimulate restoration activities, they need to be treated with caution if they are to be used as a surrogate for a whole cross section of biodiversity (Caro 2010). Often the surrogate status of a species is claimed rather than substantiated, limiting the use of these target species in restoration practices.

2) Endangered species. Generally, the best motivation for focussing on a single species in restoration practices is a species threatened status. Here, priority may be set for restoring the target species habitat as well as enhancing the viability of target populations (Karjalainen 2005).

3) Functionally important species. Along with re-establishing diversity and vegetation structure in a restoration site, the restoring of ecological processes is considered an important aspect when determining the success of restoration practices, as ecological processes, such as nutrient cycling, provide important information on the resilience of the restored ecosystem (Ruiz-Jaen and Aide 2005). Restoring populations of functionally important species can assist in restoring certain ecological processes (Snyder and Hendrix 2009; Boyer and Wratten 2010).

1.3. The Seychelles giant millipede as a target species

The SGM is a large (up to 240 mm in length), charismatic and abundant, or formerly abundant, forest macro-detritivore (Fig 1.2) (Lawrence 1999) endemic to the Seychelles granitic islands (Golovatch and Gerlach 2010), making it a potential flagship species for Seychelles invertebrate conservation. It has been recorded from Seche, Isle aux Vaches Marine, Mamelles, Silhouette, Curieuse (possibly extirpated), Aride, Cousin, Cousine, Round, La Digue, Felicité, Grand Soeur, Marianne and Frégate. It formerly occurred on the main islands of Mahé and Praslin, but is now extirpated on these islands. Although no subspecies have been described, the SGM shows slight geographical variation with island populations differing in colouration, gonopod structure and leg spines (Golovatch and Gerlach 2010). The SGM is currently IUCN Red Listed as “Vulnerable” (IUCN 2011), making it of conservation significance. Furthermore, where abundant, the SGM ingests a significant proportion of the forest floor leaf litter, therefore playing a keystone role in litter breakdown and nutrient dynamics. It has been calculated that the SGM ingested 4.55 % of the litter standing crop, and 17.19 % of the daily litter fall every 24 h, with total faecal production being 2.90 % of the total litter standing crop and 10.96 % of the daily litter fall (Lawrence and Samways

2003). This large litter consumption and feacal production rate has a highly significant effect on the smaller islands which, being small and granitic, depend on nutrient cycling to maintain their ecological integrity. The restoration of the SGM is not only about conserving a threatened species, but also about conserving and/or restoring an essential ecological process. The SGM therefore fits into all three target species categories discussed above.

1.4. The Seychelles granitic islands

1.4.1. Geography

The Seychelles islands consist of ± 115 islands scattered over an area of ± 1.3 million km^2 of the western Indian Ocean (4º - 10º S; 45º - 56º E; Fig 1.3) (Tingay 1995). They can be divided into two main island types: the granitic and coral islands.

The granitic islands are made up of 40 islands scattered across ± 400 000 km^2 of ocean. These islands were part of the super-continent Pangaea, and are the only mid-oceanic islands that were not formed from coral or volcanic action. Approximately 200 million years ago, continental drift tore Pangaea apart, splitting the super-continent into Laurasia (North America, Europe, and Asia) to the north and Gondwanaland (South America, Australasia, Antarctica, Africa and the Indian subcontinent) to the south. The Seychelles granitic rocks are ± 650 – 750 million years old. About 125 million years ago, Madagascar, Seychelles and India broke away from Gondwanaland. Madagascar became an island ± 90 million years ago, with Seychelles splitting from the Indian subcontinent ± 65 million years ago (Braithwaite 1984).

Until as recently as 18 000 year ago, when sea levels were over 100 m lower than they are today (Camoin et al. 2004), the granitic Seychelles was a huge single land mass estimated to be several 10 000 km^2 in size (Cazes-Duvat and Robert 2001). Today, all that remains are the peaks of the highest mountains with a total land area now of ± 250 km^2. The highest point of these islands is on Mahé at 905 m above present sea level.

1.4.2. Climate of the granitic islands

The Seychelles experience a humid tropical climate in that annual rainfall exceeds 700 – 800 mm, and mean monthly temperatures are generally above 20 °C (Walsh 1984). In the southern hemisphere winter (May to October), the SE trade winds extend over the whole of the western Indian Ocean. In the southern hemisphere summer (December to March), the NW Monsoon extends over the Seychelles islands. During the transition months of April and November, winds tend to be light and variable.

The temperature records for Port Victoria (Mahé) may be regarded as representative for sea-level locations across the granitic Seychelles. Mean temperatures are 26.6 °C at Port Victoria. In common with

other equatorial regions, annual variations are small, being approximately 2 °C. Diurnal temperature ranges (3.6 °C) in Seychelles are much lower than in continental equatorial areas, because oceanic influences reduce maximum temperatures and increase minimum temperatures. On the mountainous granitic islands, temperature decreases as altitude increases. Up-land temperatures are about 3 – 4 °C cooler than sea-level temperatures.

Elevation and aspect also affect mean annual rainfall. Rainfall increases with elevation and also tends to be higher on north-facing slopes. Rainfall varies seasonally as well, and is closely linked to the SE trade winds and NW Monsoon periods. The SE trade winds bring dry weather to the Seychelles, whereas the NW monsoon period and transition months experience high rainfall.

1.4.3. Vegetation of the granitic islands

The following brief description of the granitic island vegetation is summarized from Piggott (1968), Procter (1984a, b) and Robertson (1989). The vegetation of Seychelles has changed dramatically since they were first colonised, due to guano mining, plantation cultivation and urban development. Originally the granitic islands were clothed with a dense covering of forest vegetation. Three main vegetation types (divided by altitude) can be recognised: 1) Moist forest; 2) Dry forest; 3) Coastal vegetation.

Moist forest: This forest type extends between 500 – 900 m a.s.l., where the annual rainfall is higher than at the coast. These high moist forests are dominated by many indigenous and endemic trees such as *Northia seychellana* Hook.f., *Dillenia ferruginea* (Baillon)Gilg, *Timonius sechellensis* (Baker)Summerhayes, *Erythroxylum sechellarum* O.E.Schultz and *Eugenia wrightii* Baker.

Dry forest: This forest type extends between 100 – 500 m a.s.l., and is characterised by less abundant moisture than the previous forest type. Many of these forests have been replaced by plantations of Santol, Tea and Mahogany. On the larger islands, the indigenous forests that remain are dominated by palms, most notably the well known Coco de Mer, *Lodoicea maldivica* (Gmel.)Pers. on Praslin.

Coastal vegetation: This vegetation type is found below 100 m a.s.l. on the coastal plain. Most of the original coastal plain vegetation has been cleared and cultivated. The coastal plain was historically dominated by trees such as *Calophyllum inophyllum* L. and *Terminalia catappa* L.. Formerly, extensive marsh and mangrove swamps were found on these low-lying coastal areas.

The vegetation of the smaller granitic islands has more in common with that on the coral islands, which tend to be dominated by widespread plants dispersed on ocean currents and tolerant to salt-spray and drought. *Pisonia grandis* R.Br. and *Ficus* species are, or were, abundant. Beach-crest vegetation consists mostly of *Scaevola sericae* Vahl, *Cordia subcordata* Lam, *Guettarda speciosa* L. and *Tournefourtia argentea* L.f.. Many of these islands were historically cleared of their indigenous vegetation for agriculture, notably coconut plantations, and are now generally overgrown with alien vegetation. However, much vegetation-based restoration is taking place on many of these smaller granitic islands, with the aim of restoring the vegetation to what it was formerly thought to be. So far, such projects have been prominent on

the islands of Cousine, Cousin, Aride and Frégate (Shah 2001; 2006; Henri et al. 2004; Samways et al. 2010a).

1.5. The study site – Cousine Island

The natural history of Cousine Island has been described in extensive detail in Samways et al. (2010a, b). Cousine is a small granitic island (4° 20' 4" S and 55° 38' 44" E) (Fig. 1.4) that is 27 ha in area, ± 1 km long, ± 400 m wide with a maximum elevation of ± 65 m.

Prior to the 1970s, Cousine was highly denuded of woody vegetation and had been exploited agriculturally, although remnants of the original vegetation still remained. In the early twentieth century, Cousine was covered with coconut plantations (Diamond 1975). At various times, other crop plants, including tobacco and cotton were grown. Various livestock were also kept, including cattle, pigs and chickens. Poaching of Shearwater birds (*Puffinus* species), Sooty tern eggs (*Sterna fuscata* Linnaeus) and turtle eggs (*Eretmochelys imbricata* (Linnaeus) and *Chelonia mydas* (Linnaeus)) was also prevalent. Historically cats were abundant on the island, although the island has always been free of other alien invasive mammals such as rats and mice.

In general terms, there have been three phases in the restoration of Cousine: 1) mid 1970s to the early 1990s, which focused on stopping the poaching and included the eradication of the cats; 2) early 1990s to the late 1990s, which formed the initial phase of the restoration of the coastal plain by the removal of alien vegetation (except for a small demarcated agricultural area) and the planting of indigenous vegetation; 3) late 1990s until present, which focused on furthering the vegetation-based restoration efforts initially started in the 1990s (Fig. 1.5), and control of the invasive African big-headed ant, *Pheidole megacephala* (Fabricius) (Gaigher et al. 2012).

The value of studying the SGM on Cousine is that this island is the only granitic Seychelles island that has historically always been free of alien invasive rodents (Samways 2000). Furthermore, Cousine's restoration programme is well documented making historical comparisons feasible. Moreover, Cousine falls within the Madagascar biodiversity hotspot (Myers et al. 2000), and is itself considered a 'Key Biodiversity Area' within Seychelles (Gerlach 2008b), making it an important conservation island.

1.6. Aims and dissertation structure

The broad objectives of this dissertation were to investigate selected aspects of the restoration ecology of the SGM. The intention of this project was to provide detailed information on the SGM's autecology in order to make practical restoration recommendations that can be used to assist in the conservation of this

species. This project was carried out in the context of the restoration programme that is currently taking place on Cousine Island, Seychelles.

This dissertation consists of six chapters. This chapter (Chapter 1) provides the background and aims of the project. Chapter 2 looks at the basic population dynamics of the SGM and its implications for potential translocations. Chapters 3 -5 primarily focuses on the autecology of the SGM and how restoration practices can benefit the conservation of the SGM. The concluding Chapter 6 summarises the findings of each main chapters (i.e. Chapters 2 – 5) and presents a general discussion on what the results from Chapters 2 -5 mean for restoration ecology.

A brief outline of the objectives of each chapter follows. Here I explain how each chapter helps to achieve the overall aim of the dissertation, how each chapter will build from the preceding chapters and how all the chapters fit together.

Chapter 1: Introduction.

This chapter will outline the rationale, aims and objective of this dissertation, as well as provide background information on the SGM and the geography, climate and vegetation of the Seychelles islands. As most restoration practices have failed to attract the desired fauna due to the specific habitat requirements of the desired fauna not being met, this study aims to take a species specific view to restoring habitat for a target species. This is because habitat is a species specific concept and most restoration practice aim to recreate a desired biotope (generally a vegetation type).

Chapter 2: Population dynamics of the SGM and its implications for potential translocation to suitable islands.

The objective of this chapter was to gain an understanding of the population dynamics (i.e. inter-annual and seasonal density dynamics, and demographic dynamics) of the SGM in its undisturbed indigenous forest habitat. This chapter helps to achieve the overall aim of this dissertation by providing information that can be used if translocations of the SGM to suitable areas (including restored areas) are required. This is especially applicable for the SGM which seems unlikely of inter-island dispersal. In order for translocations to stand any chance of being successful, the detailed habitat requirements of the target species need to be understood. The following three chapters will look at the habitat requirements of the SGM in a restoration context.

Chapter 3: Effect of alien vegetation on the behavioural ecology of the SGM.

The objective of this chapter was to identify the threats (i.e. alien bamboo and coconut) the SGM faces on Cousine, and to identify how restoration practices can be used to minimise these threats. Identifying these threats was done by assessing and comparing the behavioural ecology of the SGM in bamboo and coconut forest stands with that in a reference natural forest. Here, it was found that bamboo and coconut stands were unsuitable as habitat for the SGM, and it was recommended that these alien vegetation types be removed

and replaced with natural indigenous trees. However, once a threat has been identified and the recommended management action taken place to minimise the threat, we need to then assess whether the management action taken was actually suitable.

Chapter 4: Response of the SGM to forest restoration practices.
This chapter follows on from the previous chapter were it was recommended that alien vegetation types be removed and replaced with indigenous forest. Here, in this chapter I investigated how successful the forest restoration programme was in creating suitable habitat for the SGM. This was done by comparing temporal and spatial patterns of SGM population density, physical condition and behavioural attributes in the restored site with these attributes in an adjacent natural site. Here, it was found that the restored forest was not suitable as habitat for the SGM. Understanding why the management action failed to achieve the desired result is important for redirecting any future management plans and leads to the research described in chapter 5.

Chapter 5: Understanding why the SGM failed to successfully colonise the restored forest on Cousine.
The objective of this chapter was to discover why a vegetation-based approach to habitat restoration failed for the SGM. This was done by investigating which surface elements (this millipede is primarily a surface dweller) other than vegetation limited SGM densities in the restored forest. It was found here, that granitic rock crevices formed essential habitat elements for the SGM and that a vegetation-based view (i.e. a biotope-based approach) to restoring habitat for this species failed to provide some essential habitat elements. It is then recommended that if restoring habitat for target invertebrates is to be successful, we need to move from a primarily biotope-based (e.g. vegetation-based) approach to a method that focuses on both the biotic and abiotic resources that are essential for that target species survival. This concept would not only apply to the SGM but to all habitat restoration projects.

Chapter 6: Summary and conclusions.
In this final chapter I summarise the work of the previous four chapters. I then consider the global significance of this work and how it stands in the invertebrate restoration literature. As there is still much to be learnt about the conservation and restoration of this species I briefly discuss future work that needs to be carried out.

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(a)

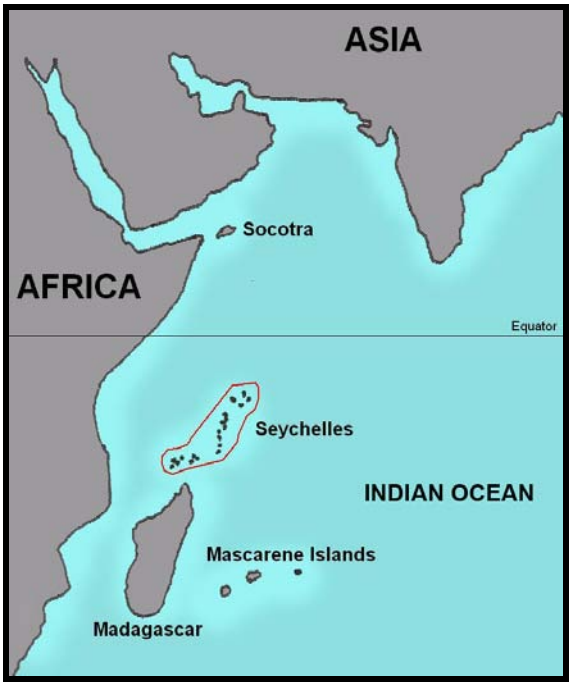
(b)

Fig. 1.1 a Seychelles giant millipede, *Sechelleptus seychellarum*, individual, with 10 cm scale bar; **b** Seychelles giant millipede feeding on fallen *Pisonia grandis* leaf litter, with 10 cm scale bar

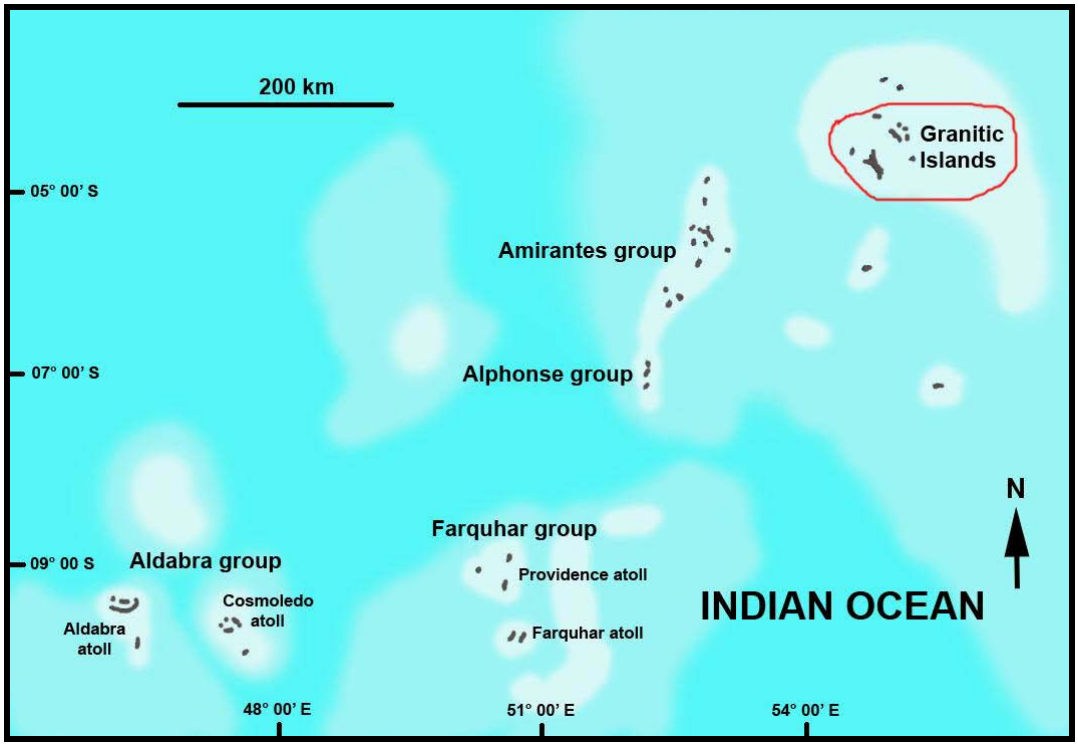
(a)

(b)

Fig. 1.2 a Forest biotope on Cousine Island, Seychelles, illustrating the habitat type of the Seychelles giant millipede; **b** granitic rock crevices are important micro-habitat elements for the Seychelles giant millipede, by forming day-time refuges



(a)



(b)

Fig. 1.3 a Map of the Indian Ocean showing the position of the Seychelles islands; **b** Map of the Seychelles islands showing the position of the granitic islands, with 200 km scale bar

Fig. 1.4 Cousine Island, Seychelles (October 2005)

(a)

(b)

Fig. 1.5 a Restoration site in March 1998 at the beginning of this project; **b** restoration site in April 2009 at the end of this project

CHAPTER 2

Population dynamics of a threatened giant millipede: implications for restoration

Abstract

The population dynamics of threatened invertebrates has important implications for their conservation, restoration and translocations. The Seychelles giant millipede (SGM), *Sechelleptus seychellarum* is a threatened and functionally important macro-detritivore endemic to the Seychelles granitic islands. Here, I studied the population dynamics of the SGM from 1998 to 2009 on Cousine Island, Seychelles, to make practical restoration recommendations. Large fluctuations in millipede densities were found between 1998 and 2009. In 2002, 2003, 2005 and 2007 millipede densities were low, while densities were high in 1998 and 2009. Although the SGM is active all year round, millipede surface activity was positively correlated with rainfall, with density being high during the wet NW monsoon period (i.e., October to April) and low during the dry SE trade wind period (i.e., May to September). Female:male:juvenile ratios were ~ 3:1:1. The implications of these results for restoration are that translocations should preferably be done in years of high millipede densities and during the wet season. Furthermore, chemical control of the invasive ant, *Pheidole megacephala*, which is currently being carried out on Cousine Island and in future could be conducted on other Seychelles islands, should preferably be done during the low rainfall months, as the SGM readily consumes the hydramethylnon-based bait.

Additional key words Seychelles; *Sechelleptus seychellarum*; sex ratios

2.1. Introduction

Field research in population biology tends to be of short duration, which often limits our understanding of a species' ecology (Ehrlich & Murphy 1987). Short-term 'snapshot' studies give little indication of a target

species' population dynamics. This can have important implications for the successful conservation and monitoring of threatened invertebrates (New 2009).

The Seychelles giant millipede (SGM), *Sechelleptus seychellarum* (DESJARDINS 1834) (Diplopoda: Spirostreptidae) (Fig. 2.1), is a very large (up to 240 mm in length) and abundant, or formerly abundant, forest macro-detritivore (Lawrence 1999) endemic to the Seychelles granitic islands (Golovatch & Gerlach 2010). It is currently IUCN Red Listed as "Vulnerable" (IUCN 2011). On the main islands of Mahé and Praslin, which are infested with potential predators, particularly *Tenrec* spp., it has been extirpated (Gerlach 2008a). Large population declines between 1998 and 2003 were recorded on several of the low-lying granitic islands (Gerlach et al. 2005), making monitoring of this invertebrate's population dynamics a conservation priority.

Tropical millipedes play an important part in the decomposition of litter material through fragmentation, facilitating the chemical breakdown of organic material by micro-organisms (Reddy 1995). This is true of the SGM, where large populations ingest a significant proportion of the litter standing crop and daily litter fall, thereby playing a keystone role in litter breakdown and nutrient dynamics (Lawrence & Samways 2003).

Despite this invertebrate's conspicuousness, threatened status and functional importance, very little is known about its basic ecology. This lack of information is also true of most tropical millipede species. By providing baseline ecological data, I aim here to evaluate the population density dynamics of this species on Cousine Island, Seychelles, to make practical restoration recommendations. As the SGM is primarily a ground dwelling invertebrate incapable of inter-island dispersal, the results here are discussed in terms of what they mean for potential translocation of this species. Although there are relatively few published examples of invertebrate translocations, with most focussing on Lepidoptera (New 2009), recently more invertebrates are being translocated or being considered for translocation to assist in their conservation (e.g. Hochkirch et al. 2007; Stringer and Chappell 2008; Watts et al. 2008). This study was carried out over an 11 year period between 1998 and 2009. The value of studying this species on Cousine is that it is the only granitic Seychelles island that is free of alien invasive mammals (Samways 2000). Furthermore, Cousine falls within a biodiversity hotspot (Myers et al. 2000), and is itself considered a 'Key Biodiversity Area' within Seychelles (Gerlach 2008b).

2.2. Methods

2.2.1. Study site

Cousine Island is a small granitic island (4° 20' 4" S and 55° 38' 44" E) (Fig. 2.2) that is 27 ha in area, ~ 1 km long, 400 m wide with a maximum elevation of 65 m. The Seychelles islands experience a tropical climate, and although considered non-seasonal, the summer NW monsoon from October to April (range

160 mm – 398 mm at sea level, Mahé) brings higher rainfall than the winter SE trade winds from May to September (range 74 mm – 170 mm) (Walsh 1984).

Three main vegetation types were identified on Cousine: 1) Natural indigenous forest (14 ha) dominated by *Euphorbia pyrifolia* LAMARCK 1788, *Ficus reflexa* THUNBERG 1786, *F. lutea* VAHL 1805, *Pisonia grandis* BROWN 1810 and *Pandanus balfouri* MARTIUS 1887 trees; 2) Restoring/restored forest which consisted of a coastal plain (6 ha) that was previously used for agriculture and livestock farming. Forest probably occupied the coastal plain, a historical condition to which it has been restored by high density planting of indigenous saplings (Samways et al. 2010); 3) Agricultural area (1 ha) which is situated in the centre of the island, and was dominated by the grass *Cynodon dactylon* (LINNAEUS 1753) PERSOON 1805 throughout the study period; the grass was mowed regularly.

2.2.2. Inter-annual population and seasonal activity dynamics

Inter-annual millipede surface densities were determined in 380 1×10 m transects in six survey periods between 1998 and 2009: February 1998 – April 1998; October 2002; February 2003 – April 2003; October 2005; February 2007 – March 2007; April – May 2009. As the life-history biology of the SGM is not known, surface density was used as a practical indicator of population numbers. The positions and orientations of the transects were randomly chosen to cover as much of the natural forest portions of the island as possible. Millipedes were only sampled in the natural forest as this area is considered the natural habitat region of the SGM, with the agricultural and restoring/restored forest considered unsuitable (Lawrence 1999). For the 1998 (n = 120) survey, the starting point of each transect was randomly selected in areas of different dominant vegetation type. Using GPS, each transect was begun at the intersection point of a hypothetical 50×50 m grid overlay for the 2002 (n = 40), 2003 (n = 100), 2005 (n = 40), 2007 (n = 40) and 2009 (n = 40) surveys.

To determine seasonal surface activity dynamics, 22 fixed 1×10 m transects were selected, as described above, in June 2002. These transects were walked in the natural forest-covered areas each month between June 2002 and April 2003 for a total of 242 surveys. As the SGM is primarily nocturnal, mean ± SD millipede surface densities (ind.m^{-2}) were determined between 20:00 and 22:30 by counting the number of individuals per transect. Daily rainfall was recorded between 1997 and 2010 using a standard rain gauge.

2.2.3. Demographic dynamics

A total of 1254 millipedes were randomly selected from the natural forest-covered areas during the 1998 (n = 211), 2003 (n = 403), 2007 (n = 324) and 2009 (n = 316) survey periods. Where millipede density was high, a 0.25 m^2 quadrat was used to randomly select individuals. All millipedes were classed as male, female or juveniles. Males were distinguished from females by the presence of gonopods (external secondary genitalia) or absence of legs on the seventh body segment (Lawrence 1984), and were more

slender. Juveniles were smaller (i.e. between 90 and 110 mm) than adult males and females. Millipedes smaller than 90 mm were rarely seen on the soil surface. The percentages of male, female and juveniles in each survey period were calculated.

2.2.4. Statistical analyses

All statistical analyses were carried out using STATISTIXL 1.8 (2007) software (available at www.statistiXL.com). Non-parametric inferential tests were used as data did not always satisfy parametric assumptions (Gardener 2011). Kruskal-Wallis Tests were used to test for significant differences in mean annual millipede density (1998 to 2009) and mean monthly millipede density (June 2002 to April 2003). Spearman rank correlation r_s tests were used to test for any significant correlations between mean monthly millipede density and rainfall (June 2002 to April 2003); and between time and the percentage of female millipedes (1998 to 2009). Mann-Whitney U Tests were used to test for significant differences in millipede densities between: 1998 and 2002; 2002 and 2003; 2003 and 2005; 2005 and 2007.

2.3. Results

2.3.1. Inter-annual millipede density dynamics

The population densities of the SGM in the natural forest areas on Cousine fluctuated significantly over the study period between a mean ± SD of 9.98 ± 3.23 ind.m^{-2} (n = 40) in 2009 and 0.84 ± 0.32 ind.m^{-2} (n = 40) in 2002 (Kruskal-Wallis Test, $P < 0.001$; n = 380; Fig. 2.3). Mean millipede density dropped significantly between 1998 and 2002 (Mann-Whitney U Test, $P < 0.001$; n = 160), but then showed an obvious increase from 2003 to 2009. No significant differences were found in mean millipede population density between 2002 and 2003 (Mann-Whitney U Test, n.s.; n = 140) and between 2005 and 2007 (Mann-Whitney U Test, n.s.; n = 80). However, there was a significant increase in mean millipede density from 2003 to 2005 (Mann-Whitney U Test, $P < 0.05$; n = 140).

2.3.2. Seasonal millipede population dynamics

The monthly population densities of the SGM in the natural forest areas fluctuated significantly over the 11 month period (Kruskal-Wallis Test, $P < 0.001$; n = 242; Fig 2.4). Lowest densities were recorded between June and August which coincided with the low rainfall period. Millipede densities were highest between September and April which coincided with the high rainfall months. A significant positive correlation was found between mean monthly millipede surface density and total monthly rainfall ($r_s = 0.565$; Spearman Rank Correlation, $P < 0.05$; n = 11).

2.3.3. Demographic dynamics

The SGM population on Cousine throughout the study period consisted of more females (mean: 57.21%) than males (mean: 21.32%) and juveniles (mean: 21.47%) (n = 1254; Fig. 2.5). Female:male:juvenile ratios were ~ 3:1:1. Although the percentage of females varied from a high of 66.44% in 1998 to a low of 44.62% in 2009, this trend was not significant (r_s = -0.8; Spearman Rank Correlation. n.s., n = 4).

2.4. Discussion

2.4.1. Population dynamics

The population densities of the SGM decreased significantly from 1998 to 2002 on Cousine. Similar trends were also reported on the low-lying granitic islands of Aride and Frégate, resulting in concerns over whether the species was in decline. While it is thought that SGM population density fluctuates inter-annually in response to rainfall variations or sarcophagid parasitism (Gerlach et al. 2005), these data are limited and not conclusive, making an understanding of the underlying causes of these fluctuations unclear. This is further compounded by our poor knowledge on the life-history development and requirements of these long-lived spirostreptid species (Crawford et al. 1987; Enghoff et al. 1993). However, millipede population densities began to gradually increase on Cousine from 2005 onwards, with 2009 densities exceeding those in 1998. No long-term population monitoring has been conducted on Aride or Frégate so it is unclear whether millipede numbers returned to similar pre-decline densities on these islands.

Although the SGM is active all year round, it still nevertheless showed seasonal surface density fluctuations in relation to rainfall patterns, with millipedes more abundant on the surface during the high rainfall NW monsoon period. Such rainfall-related seasonal activity patterns are well known for Indian (Bhakat 1987; 1989; Ashwini & Sridhar 2006) and southern African millipedes (Dangerfield & Telford 1991; Dangerfield et al. 1992). Millipedes are highly susceptible to desiccation and have evolved a variety of behavioural mechanisms to reduce water loss (Hopkin & Read 1992). Millipedes select areas with favourable temperature and humidity conditions to avoid unsuitable microclimates (e.g. Cloudsley-Thompson 1950; Edney 1950; Toye 1966; Berġholz 2007). Furthermore, burrowing has been shown to be an important behavioural response to moisture and temperature stress for the large spirostreptid millipede *Alloporus uncinatus* (ATTEMS 1914) (Dangerfield & Chipfunde 1995). However, whether the SGM burrows during the drier SE trade wind period is not known.

Millipede sex ratios tend to be species-specific. Similar to the findings of Rantala (1974) for *Proteroilus fuscus* (AM STEIN 1857), females of the SGM were more common than males and juveniles. In contrast, both Morse (1903) and Ramsey (1966) found a predominance of juvenile millipedes in *Parajulus*

pennsylvanicus (BRANDT 1840) and *Pseudopolydesmus serratus* (SAY 1821) swarms respectively, while Lawrence (1952) found that a *Orthoporus (Gymnostreptus) pyrrocephalus* (KOCH 1865) swarm consisted mainly of adults with a sex ratio of close to 1:1.

2.4.2. Restoration implications

Seychelles invertebrate biodiversity, with its high levels of endemism, is largely threatened by habitat deterioration as a result of historical deforestation and alien flora (Gerlach 2008a), with < 5% of the original vegetation remaining on the granitic islands (Baider et al. 2010). Ecological restoration plays an important role in the conservation of several Seychelles islands (Henri et al. 2004; Shah 2006; Samways et al. 2010).

Many threatened invertebrates depend on some form of habitat restoration for their long-term security, where the restoration of focal species populations, either by augmentation of existing populations or establishment of new ones, can be considered an important conservation management approach (New 2009). Often these invertebrates are threatened by habitat destruction (Samways 2005) and/or alien species (Davies 2009), and translocations can have the potential to mitigate these threats by providing the species with new suitable habitat. Site isolation (Knop et al. 2011) and dispersal ability (Moir et al 2005) are two factors that often limit invertebrate colonisation of restored sites. Translocations can help overcome these limitations by assisting with the dispersal of target animals.

Although, most invertebrate translocation programmes have focussed on Lepidoptera (New 2009), several have looked at other insect orders, in particular the Orthoptera (e.g. Hochkirch et al. 2007; Stringer and Chappell 2008; Watts et al. 2008). However, other invertebrate taxa have been translocated, for example Odonata, Diptera, Phasmatodea, Annileda and Mollusca (Soorae 2010). In general, a good knowledge of the target species autecology is considered essential if translocations are to stand a chance of success (Samways 1994; Holloway et al. 2003). Even then, many fail for undetermined reasons (Oats and Warren 1990; Fischer and Lindenmeyer 2000). Care must be taken to not further threaten the donor population by significantly reducing their numbers unnecessarily (Bullock et al. 1996).

For the SGM, translocation to other islands is a potential option, especially as this species is currently Red-Listed, and it would certainly play an important role in nutrient dynamics on these islands. Furthermore, the SGM seems to be incapable of inter-island dispersal, making translocation the only viable option to moving individuals to other islands. Unfortunately the main islands of Mahé and Praslin would be unsuitable due to the persistence of extinction factors (i.e. habitat destruction from urban growth and the presence of many exotic species such as rats and *Tenrec* spp.). Other islands such as North Island and Curieuse Island would certainly have potential for future possible translocation efforts if required.

Although no subspecies of the SGM have been described, this species does show slight geographical variation with island populations differing in colouration, gonopod structure and leg spines (Golovatch and Gerlach 2010). Genetic differences in the SGM are quite likely as the granitic islands have

been isolated from each other for ca. 18 000 years (Cazes-Duvat and Robert 2001; Camoin et al. 2004). Care must be taken with the supplementation and the spread of translocated individuals and their progeny into resident populations on other island's as they may affect the genetic structure of that islands wild population (Bullock et al. 1996).

Based on the results presented here, the following restoration recommendations are made:

- as millipede densities fluctuate inter-annually, where possible, population augmentation and/or establishment should be done when millipede densities are high so as to reduce the risk to the donor population.
- as millipede surface activity is highest during the high rainfall NW monsoon period, population augmentation and/or establishment should be done during this period to improve the chances of successful establishment.
- translocated or augmented populations should aim to comprise a 3:1:1 female:male:juvenile ratio.
- as part of the island restoration programme, control of the invasive African big-headed ant, *Pheidole megacephala* (FABRICIUS 1793), has been undertaken with the use of the hydramethylnon-based bait Siege (Gaigher et al. 2011). While the SGM readily ingests the bait and appears not to be harmed in the short-term (Lawrence et al. 2011), the long-term impacts of bait ingestion on the millipede are not known. Also, ant bait is now being administered via bait stations to reduce SGM access to the bait (Gaigher et al. 2012). However, as a further precaution, it is recommended that baiting of the ant be mostly confined to low rainfall months when millipede surface activity is at its lowest.

While I am not suggesting that the SGM must be translocated to other islands for its continued survival, the data presented here provide some population guidelines for such a conservation management approach. Further research on why SGM numbers fluctuate, possible sub-speciation and genetic difference among island sub-populations, as well as describing and understanding its life-history requirements should be considered a conservation priority.

2.5. References

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Fig. 2.1. The Seychelles giant millipede, *Sechelleptus seychellarum*, with 10 cm scale bar.

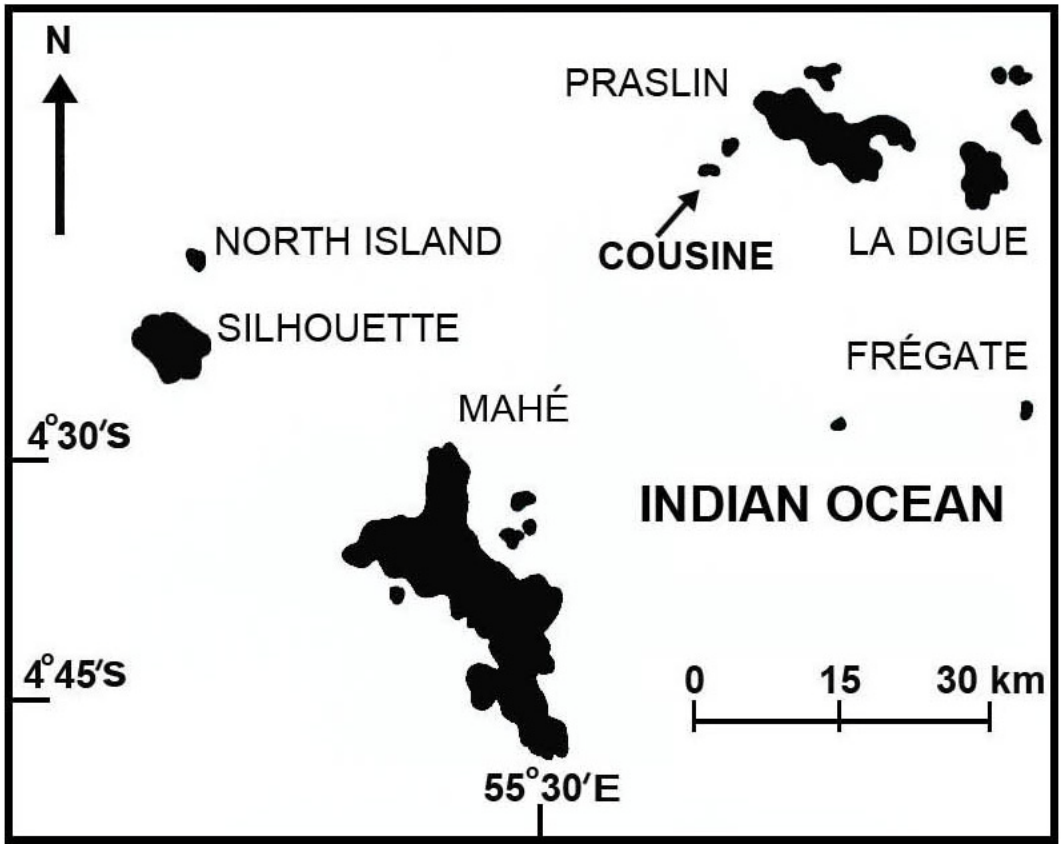

Fig. 2.2. Central group of Seychelles granitic islands, showing the position of Cousine Island, Seychelles.

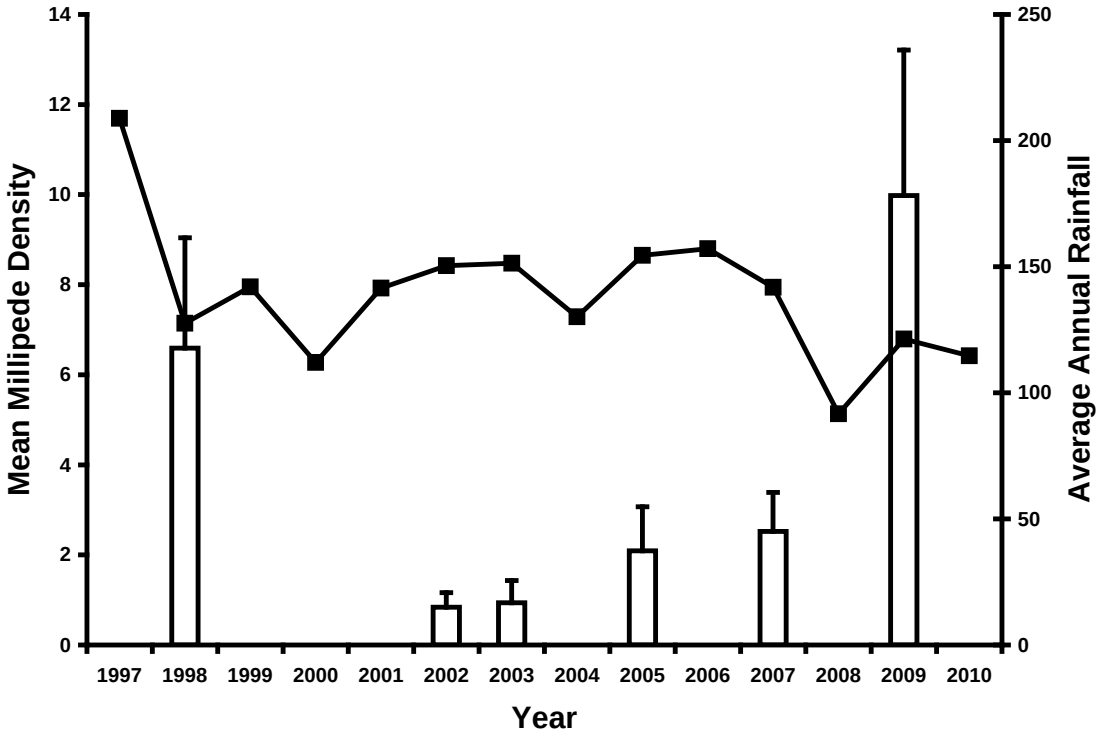

Fig. 2.3. Inter-annual mean ± SD millipede surface density (ind.m^{-2}) (*White bar*) and average annual rainfall (mm) (*Black line*) on Cousine Island, Seychelles between 1997 and 2010. Millipede data only collected 1998, 2002, 2003, 2005, 2007 and 2009.

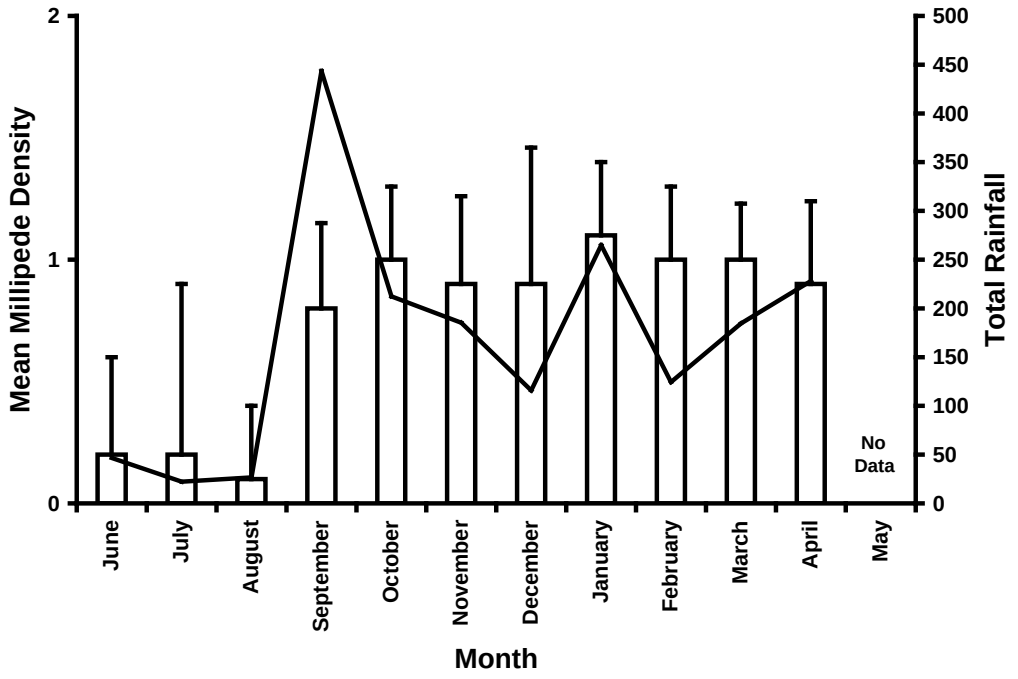

Fig. 2.4. Seasonal relationship between millipede surface density and rainfall on Cousine Island, Seychelles, between June 2002 and April 2003. *White bar* mean ± SD millipede density (ind.m^{-2}); *Black line* total monthly rainfall (mm).

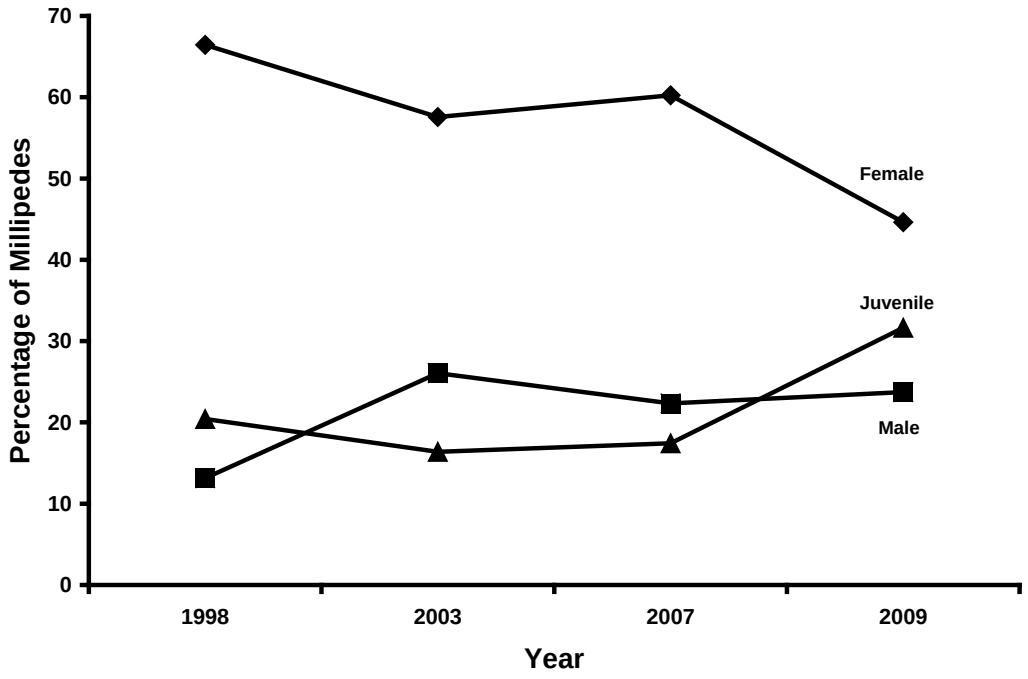

Fig. 2.5. Seychelles giant millipede population demographic dynamics between 1998 and 2009 on Cousine Island, Seychelles. *Diamond* percentage females; *Square* percentage males; *Triangle* percentage juveniles.

CHAPTER 3

A behavioural ecology approach to assessing the effect of alien vegetation on a threatened giant millipede

Abstract

The importance of taking into account behavioural ecology when assessing the impacts of habitat deterioration on threatened species is evaluated. The Seychelles giant millipede (SGM), *Sechelleptus seychellarum*, is IUCN Red Listed as "Vulnerable". Here, I studied the effect of alien bamboo and coconut stands on the behavioural ecology of this species on Cousine Island, Seychelles in order to understand how the restoration programme can be directed to assist in the conservation of the SGM. Coconut did not affect SGM density, but negatively affected its foraging behaviour, whereas bamboo negatively affected both its density and foraging behaviour. The SGM showed feeding preferences for *Pisonia grandis* and *Ficus* sp. leaf litter types. Alien bamboo and coconut pose a varied threat to the SGM, and their removal and replacement by indigenous forest species (e.g. *P. grandis* and *Ficus* sp.) should form part of an island's restoration programme.

Keywords bamboo; coconut; foraging ecology; leaf litter; Seychelles

3.1. Introduction

Invasion by alien plant species is a global environmental problem (Greipsson 2011). Although the impact of alien vegetation on native plants is well documented (Kiehn 2011), its effect on indigenous invertebrates is less understood, and often varies depending on the plant species involved (Samways 2005). Alien plants influence the structure and physiognomy of ecosystems (Usher 1988), which may lead to an increase in the rarity and vulnerability of native invertebrates (New 1993). Understanding how these changes in vegetation

composition affect threatened invertebrate species would have significant implications for their conservation and restoration.

The Seychelles giant millipede (SGM), *Sechelleptus seychellarum* (Desjardins) (Diplopoda: Spirostreptidae) is a large (up to 240 mm in length) and abundant, or formally abundant, macro-detritivore endemic to the Seychelles granitic islands (Golovatch and Gerlach 2010). On the main Seychelles islands of Mahé and Praslin, which are infested with potential alien predators, particularly *Tenrec* species, the SGM has been extirpated (Gerlach 2008a). The SGM is IUCN Red Listed as "Vulnerable" (IUCN 2011).

Significantly, millipedes play a key role in the decomposition of organic material through the fragmentation of litter material (Hanlon 1981), facilitating the chemical breakdown of organic material by micro-organisms (Anderson and Bignell 1982). This is especially true of the SGM which, where abundant, ingests a significant proportion of the litter standing crop and daily litter fall, therefore playing a keystone role in litter breakdown (Lawrence and Samways 2003).

The SGM is still common in the indigenous forest covered areas on Cousine Island, Seychelles (Lawrence 1999). Cousine falls within a biodiversity hotspot (Myers et al. 2000) and is considered a 'Key Biodiversity Area' within Seychelles (Gerlach 2008b). Furthermore, it is apparently the only tropical island globally > 20 ha which has never had any mammal invasions (Samways 2000). Moreover, central Cousine has a relatively undisturbed tropical forest ecosystem (Samways et al. 2010). Despite the near-natural condition of the island's vegetation, some areas are still dominated by alien bamboo, *Bambusa vulgaris* Schrad. ex Wendl. and coconut, *Cocos nucifera* L.. Both bamboo and coconut are considered invasive in Seychelles (Fleischmann 1997), and are being removed or have been removed from the island through an intensive restoration programme (Samways et al. 2010).

Most studies that focus on the impact of alien flora on invertebrates rarely take into account its effect on a species' behaviour. I believe that by taking the behavioural ecology of a species into account a greater understanding is gained. Here, changes in floral structure and physiognomy due to the replacement of natural forest by bamboo and coconut were expected to influence SGM density and behaviour in areas dominated by these alien plants. Animal behaviour can play an important role in the restoration process (Lindell 2008). Understanding the impact of possible threats on a target species can help in directing restoration practices to reduce the effects of the potential threat. As a result, this study aimed to assess the comparative impact of small-scale bamboo and coconut abundance on the behavioural and foraging ecology of the SGM. Furthermore, the effect of bamboo removal on the SGM was investigated.

3.2. Methods

3.2.1. Study site

Cousine Island is a small granitic island (4° 20' 4" S and 55° 38' 44" E) (Fig. 3.1) that is 27 ha, ± 1 km long, 400 m wide with a maximum elevation of 65 m. The Seychelles islands experience a tropical climate, and although considered non-seasonal, the summer NW monsoon (i.e October to April) brings higher rainfall than the winter SE trade winds (i.e. May to September).

The vegetation of the island is mostly natural forest dominated by indigenous *Ficus reflexa* Thunb., *F. lutea* Val., *Pisonia grandis* R.Br., and *Pandanus balfouri* Mart. trees. Other tree species present are *Morinda citrifolia* L., *Calophyllum mophyllum* L. and *Euphorbia pyrifolia* Lam.. Although patchy in distribution, the most dominant ground cover is the fern *Nephrolepis biserrata* (Sw.) Schott. Single bamboo and coconut stands, each ± 0.5 ha, occur/occurred within this natural forest matrix. As part of the island restoration programme all bamboo was removed by 2009, leaving this area clear of vegetation. A coastal plain was previously used for agriculture and livestock farming. Forest probably occupied the coastal plain, a historical condition to which it has been restored by high density planting of indigenous saplings (Samways et al. 2010). A demarcated area is situated in the centre of the island, and is dominated by mowed *Cynodon dactylon* (L.) Pers. grass. All data were collected in April 2003 and April 2009.

Three sites were used in this study (Table 1): 1) a circular/oval area (± 0.5 ha) dominated by bamboo and surrounded by natural forest; 2) A circular/oval area (± 0.5 ha) dominated by coconut and surrounded by natural forest; 3) the natural forest matrix that lay between the coconut and bamboo sites (± 1.0 ha). Both the bamboo and coconut sites were comparable in size, shape, topography and surrounding vegetation. All three sites were 35 – 45 m a.s.l..

3.2.2. SGM density

Millipede surface densities were determined using 1×10 m transects. In 2003, transects were walked in the Bamboo (n = 14), Coconut (n = 14) and Natural Forest (n = 28) study sites. To determine the effect of bamboo removal on SGM density, a further 30 transects were walked in 2009 in the Bamboo (n = 10) and Natural Forest (n = 20) sites. Due to the small sizes of the alien vegetation sites, a smaller sample size had to be used in these sites to prevent pseudo-replicating transects.

As the SGM is primarily nocturnal, mean ± SD millipede surface densities (ind.m^{-2}) were determined between 20:00 and 22:30 by counting the number of individuals per transect. In order to determine the effect of bamboo removal on the SGM, the mean density of millipedes in the bamboo site was calculated relative to the mean density of millipedes in the Natural Forest site. This was done because inter-annual SGM densities fluctuated greatly (Chapter 2).

3.2.3. SGM behaviour

Behavioural observations of randomly selected individuals were made at night between 20:00 and 22:30 over six nights in the three study sites in 2003 and in the Bamboo site in 2009. Where millipede density

was high, a 0.25 m^2 quadrat was randomly placed, and the behaviour of all individuals in the quadrat recorded.

Six main behavioural types were displayed by the SGM: walking, feeding, copulating, resting, burrowing and grooming. The dominant behaviours were walking and feeding (Lawrence and Samways 2003). Walking was assumed to be associated with the search for suitable conditions and resources such as food or potential mates. Feeding consisted of individuals ingesting food items such as bark, sticks, fallen fruit, bird faeces, soil/algae, flowers, with leaf litter making up the largest percentage (i.e. ± 55 %) of all feeding observations (Lawrence and Samways 2003). As the other four behaviour types were rarely observed, their results are only briefly mentioned in this study.

The mean ± SD percentage of SGM individuals over the six nights displaying the walking and feeding behaviour types relative to the total number of behaviour observations (i.e. for all six behaviour types) were calculated for each study site. A total of 532 walking and feeding observations were made during the 2003 (n = 410) and 2009 (n = 122) survey periods.

3.2.4. Leaf litter selection

During the 2003 survey period, the species of leaf litter on which randomly selected millipedes were feeding was sorted as follows: *P. grandis*; *Ficus* sp.; *P. balfouri*; *B. vulgaris*; *C. nucifera*; 'Other'. The category 'Other' included leaf litter species that were seldom sampled (e.g. *M. citrifolia*, *C. mophyllum*, *N. biserrata*, and unidentified species). The percentage of millipedes feeding on each leaf litter type in the Bamboo (n = 141), Coconut (n = 233) and Natural Forest (n = 305) study sites was calculated. A total of 679 observations were made.

3.2.5. Leaf litter composition

During the 2003 survey, the leaf litter composition in the Bamboo (n = 10); Coconut (n = 10) and Natural Forest (n = 20) study sites was determined using a 0.25 m^2 quadrat. All leaf litter in each quadrat was sorted into the five leaf litter categories described above, air dried and weighed to the nearest 0.2 g using a portable Pisola spring scale. The percentage of each leaf litter type per study site was calculated.

3.2.6. Statistical analyses

All statistical analyses were carried out using STATISTIXL 1.8 (2007) software. Non-parametric inferential tests were used as data did not satisfy parametric assumptions (Siegel and Castellan, 1988). Mann-Whitney U Tests were used to test for any significant difference in mean: millipede density between the Bamboo, Coconut and Natural Forest sites in 2003; percentage of walking and feeding observations

between the Bamboo, Coconut and Natural Forest sites in 2003; percentage of walking and feeding observation in the Bamboo site between 2003 and 2009.

3.3. Results

3.3.1. SGM density

Mean millipede density in 2003 varied between the three study sites (Fig. 3.2). Millipede density was highest in the Natural Forest site (Mean ± SD: 1.78 ± 1.26 ind.m^{-2}; n = 28) and lowest in the Bamboo site (Mean ± SD: 0.20 ± 0.44 ind.m^{-2}; n = 14). Although millipede density was lower in the Coconut site (Mean ± SD: 1.43 ± 0.51 ind.m^{-2}; n = 14) compared with the Natural Forest site, this difference was not significant (Mann-Whitney U Test; n.s.).

3.3.2. SGM behaviour

The mean percentage of millipedes in the Natural Forest (Mean ± SD: 7.17 ± 2.64 %; n = 6) displaying the walking behaviour was significantly lower than the percentage of millipedes displaying the walking behaviour in the Bamboo (Mean ± SD: 36.84 ± 4.54 %; n = 6; Mann-Whitney U Test, $P < 0.01$) and the Coconut (Mean ± SD: 27.50 ± 5.32 %; n = 6; Mann-Whitney U Test, $P < 0.01$) sites. Furthermore, significantly more millipedes displayed the walking behaviour in the Bamboo compared with the Coconut site (Mann-Whitney U Test, $P < 0.05$) (Fig. 3.3).

The percentage of millipedes in the Natural Forest (Mean ± SD: 84.84 ± 4.17 %; n = 6) displaying the feeding behaviour was significantly higher than the percentage of millipedes displaying the feeding behaviour in the Bamboo (Mean ± SD: 52.84 ± 6.05 %; n = 6; Mann-Whitney U Test, $P < 0.01$) and the Coconut (Mean ± SD: 65.17 ± 7.47 %; n = 6; Mann-Whitney U Test, $P < 0.01$) sites. Furthermore, significantly fewer millipedes displayed the feeding behaviour in the Bamboo compared with the Coconut site (Mann-Whitney U Test, $P < 0.05$) (Fig. 3.3).

The other four behaviour types were rarely sampled. In the Natural Forest, Bamboo and Coconut sites these other behaviours comprised the following percentage of the observations respectively: Copulating = 0.21 % / 0.00 % / 0.17%; Resting = 1.19 % / 4.61 % / 3.81 %; Burrowing = 3.65 % / 4.06 % / 2.01 %; Grooming = 2.94 % / 1.65 % 1.34 %.

3.3.3. Leaf litter selection

Pisonia grandis and *Ficus* sp. were the most commonly selected leaf litter type in all three study sites (Fig. 3.4). No millipedes were observed feeding on the bamboo and coconut leaf litter despite it being the most

abundant litter available in these sites respectively. Furthermore no millipedes were observed feeding on the *P. balfouri* litter even though it was readily available in the Natural Forest site.

3.3.4. Effect of bamboo removal on SGM density

In 2003, mean relative millipede density in the bamboo area compared with that in the natural forest was 11.24 % (n = 42). By 2009, after all bamboo was removed, mean millipede relative density in the ex-bamboo area decreased to 9.23 % (n = 30). This decrease was not significant (Mann-Whitney U Tests, n.s.)

3.3.5. Effect of bamboo removal on SGM behaviour

No significant differences were found between the percentage of millipedes displaying the walking behaviour in 2003 (Mean ± SD: 27.50 ± 5.32 %; n = 6) and 2009 (Mean ± SD: 37.33 ± 9.37 %; n = 6; Mann-Whitney U Test, n.s.). Furthermore, no significant differences were found between the percentage of millipedes displaying the feeding behaviour in 2003 (Mean ± SD: 65.17 ± 7.47 %; n = 6) and 2009 (Mean ± SD: 59.50 ± 9.89 %; n = 6; Mann-Whitney U Test, n.s.) (Fig. 3.5).

3.4. Discussion

SGM density was significantly lower in the Bamboo site compared with the Natural Forest site, while its density in the Coconut site was similar to that in the Natural Forest site, indicating that the impact of alien vegetation on SGM density is specific to alien vegetation type. As the Bamboo and Coconut sites were comparable in size, shape and surrounding natural forest vegetation, millipedes would have had similar access to both sites. Furthermore as the SGM is readily mobile, travelling between 20 – 60 m per 24 hr (J. Lawrence, unpubl. data), millipedes would have easily been able to enter these sites from the surrounding natural forest matrix.

Bonham et al. (2002) found millipedes to be less diverse in Tasmanian plantations compared with native forests. In contrast, millipede abundance was not affected by Giant Knotweed, *Reynoutria* sp., invasive in Germany (Kappes et al. 2007). Replacement of the native forest with bamboo and coconut would lead to the homogenisation of the vegetation composition and structure. Such changes influence invertebrates, by altering microclimate conditions (Samways and Moore 1991; Samways et al. 1996), three-dimensional habitat structure (Pearson 2009) and food availability (Braby and Dunford 2007).

Alien vegetation has been shown to affect invertebrate behaviour (e.g. Lawrence and Samways 2002), although few studies have taken this aspect into account when assessing the effect of habitat deterioration on threatened invertebrates. Here, alien vegetation clearly affected the behaviour of the SGM. Compared to the natural forest, fewer millipedes were observed feeding in areas dominated by bamboo and

coconut vegetation, with more millipedes observed walking in these areas, suggesting there was a lack of suitable food resources in these sites.

A clearer picture can be gained by looking at the leaf litter preference of the SGM in relation to the leaf litter species available. The SGM showed clear preferences for certain species of leaf litter. *Pisonia grandis* and *Ficus* sp. was the most commonly selected leaf litter type in all three study sites, despite these leaf litter species being the primary leaf litter available to the SGM in the Natural Forest site only. Millipedes were not seen feeding on *B. vulgaris*, *C. nucifera* and *P. balfouri*, even though the latter is endemic to Seychelles (Matatiken and Dogley 2006). Due to the small area of the alien vegetation patches, small quantities of *Pisonia* and *Ficus* leaf litter were found in the Bamboo and Coconut sites, most likely windblown from the surrounding natural forest matrix.

This preference for specific leaf litter species by the SGM is not surprising as it is well known that millipedes show preferences for certain leaf litter species (Kheirallah 1979; Ashwini and Sridhar 2005). Such preferences have been attributed to the phenolic and moisture content, as well as the C:N ratio of the leaf litter (Hopkin and Read 1992). While the chemical composition of *P. grandis* and *Ficus* sp. leaf litter on Cousine is not known, SGM individuals were often observed feeding on freshly fallen litter as opposed to older dry leaf litter, suggesting moisture content was an important selection factor here. Furthermore, Barlow (1957) found that a certain degree of 'softness' was required to overcome the limitations of the millipede chewing mechanism. This is supported by the observations that SGM individuals were most often recorded feeding on soft *P. grandis* and *Ficus* sp. leaf litter, with millipedes not seen feeding on the tough and dry *B. vulgaris*, *C. nucifera* and *P. balfouri* leaf litters. However, in contrast to this study, Ashwini and Sridhar (2005) found that the millipede *Arthrosphaera magna* Attems preferred coconut leaf litter over other leaf litter types offered in microcosm feeding trials.

As part of the island restoration programme, by 2009 all bamboo was removed from Cousine (Samways et al. 2010), with several indigenous tree saplings (i.e. ± 0.5 – 1.0 m in height) being planted in the cleared ex-bamboo area. SGM density and behaviour in the ex-bamboo area was similar to what it was when the bamboo was present, indicating that millipedes viewed the cleared ex-bamboo area in the same way they viewed the bamboo stand. This was not unexpected, as the SGM is generally associated with a forest biotope (Lawrence 1999). On the contrary, Samways and Sharratt (2009) found natural and cleared sites to be more similar in invertebrate abundance and richness compared with sites dominated by alien vegetation. Although the time-span of this study was insufficient for the establishment of a closed canopy natural forest in the ex-bamboo site by the planted saplings, once this canopy closure is reached it is likely that millipede density and behaviour would be similar to that in the natural forest.

These results have important conservation and restoration implications. Seychelles invertebrate biodiversity, with its high levels of endemism, is largely threatened by habitat deterioration as a result of historical deforestation and invasive exotic flora (Gerlach 2008a). Less than 5% of the original vegetation remains on these islands (Baider et al. 2010), with the native forests being threatened by the invasion of introduced plants (Fleischmann 1997). Ecological restoration plays an important role in the conservation of

several Seychelles islands (Henri et al. 2004; Shah 2006; Samways et al. 2010), and can potentially play a vital part in reversing or reducing these impacts.

Many threatened invertebrates rely on some form of habitat restoration for their long-term security (New 2009). This can be particularly important for endemic island invertebrates, which frequently have small population sizes, further limited by a lack of suitable habitat (New 2008). However, an important part of restoring habitats for threatened species is to be able to positively identify the threats, so an effective conservation management programme can be actioned.

Although I only focussed on the impact of small-scale bamboo and coconut stands on the SGM here, the impact of larger stands would be expected to be far greater. This study clearly highlights the importance of taking behaviour ecology into account when assessing the impacts of habitat deterioration on a species. While coconut did not affect SGM density it clearly affected its foraging ecology, whereas bamboo affected both its density and foraging ecology. Alien bamboo and coconut stands pose a varied threat to the SGM, and their removal and replacement by indigenous forest species (e.g. *P. grandis* and *Ficus* sp.) should form part of an islands' restoration programme. Furthermore, the existence of *P. grandis* as a dominant forest is globally rare (Gerlach 2008b). *Pisonia grandis* forests would not only benefit the SGM, but would also create further nesting sites for tree-nesting seabirds, making the restoration of such forests a conservation priority.

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Table 3.1 Vegetation description of the three study sites used in 2003 and 2009

Study site	Dominant vegetation Species	Canopy closure (%)	Vegetation height (m)	Other non-dominant vegetation species
Bamboo (2003)	*B. vulgaris*	> 65 %	5 – 10 m	None
Bamboo (2009)	None	0 %	0 %	None
Coconut (2003)	*C. nucifera*	> 60 %	8 - 10 m	*P. grandis*; *Ficus* sp.
Natural Forest (2003)	*P. grandis*; *Ficus* sp.; *P. balfouri*	> 80 %	8 – 15 m	*E. pyrifolia*; *M. citrifolia*; *N. biserrata*; *C. mophyllum*

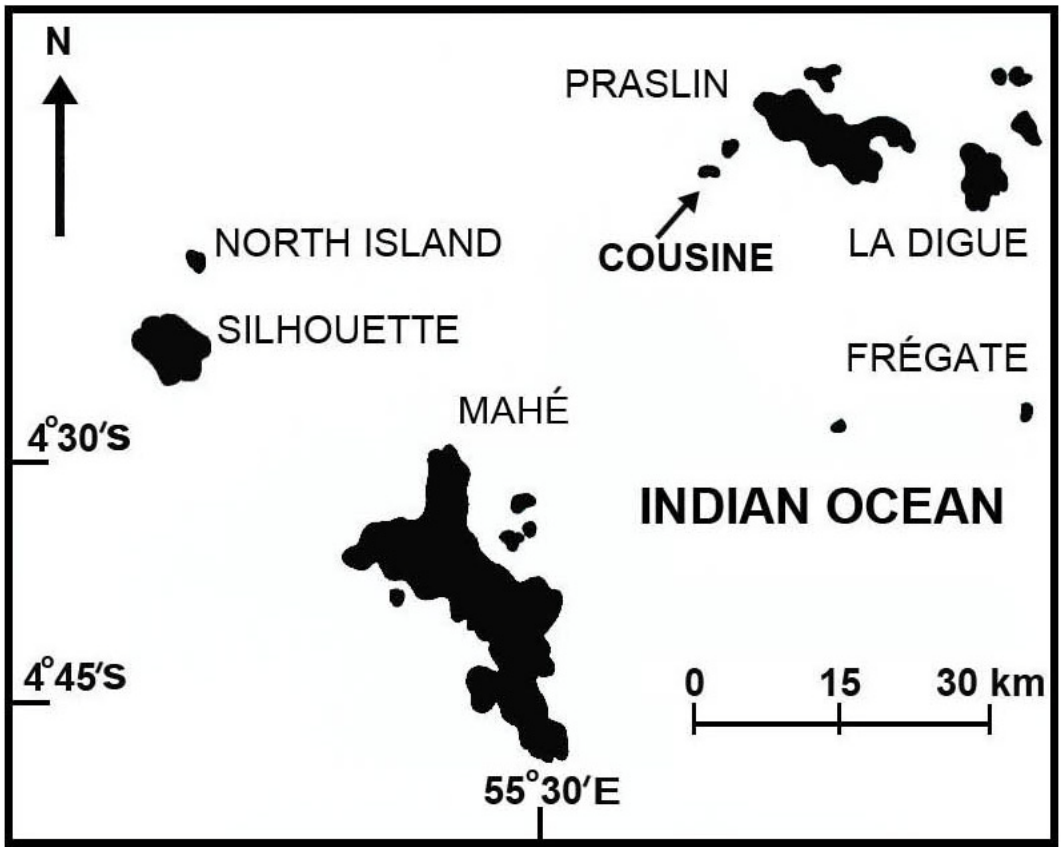


Fig. 3.1 Central group of Seychelles granitic islands, showing the position of Cousine Island

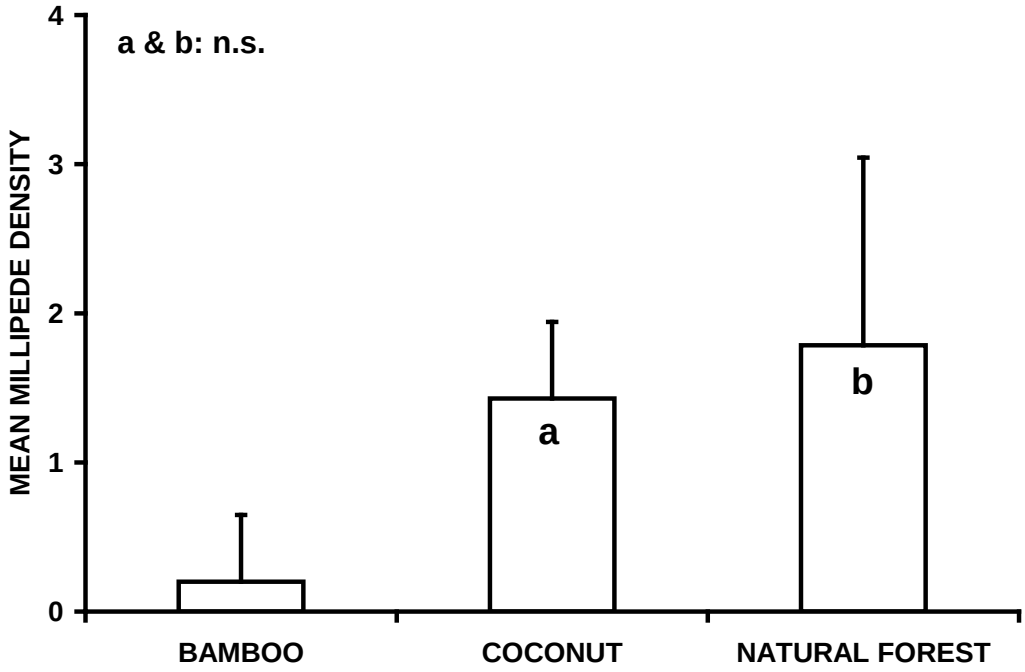


Fig. 3.2 Mean ± SD millipede density (ind.m^{-2}) in the Bamboo (n = 14), Coconut (n = 14) and Natural Forest (n = 28) study sites in 2003. Mann-Whitney U Test significant level between the Coconut and Natural Forest sites provided; n.s. not significant

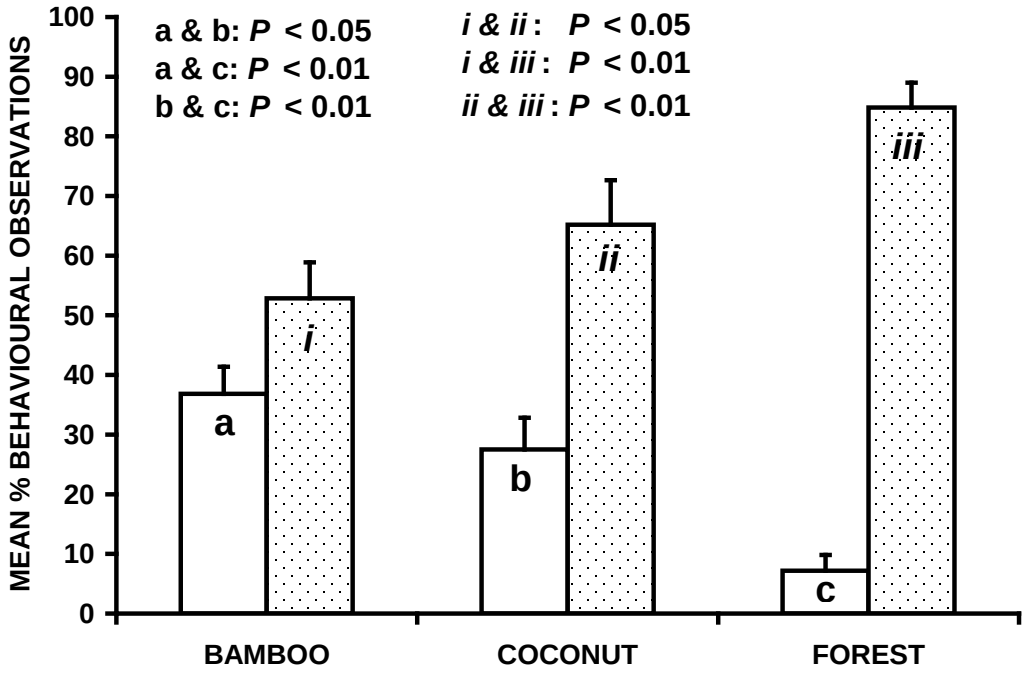
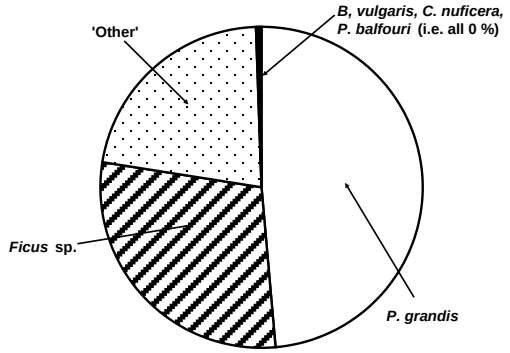
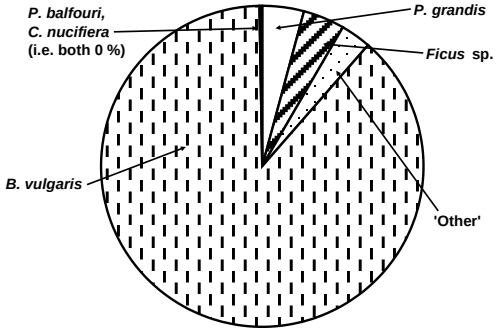


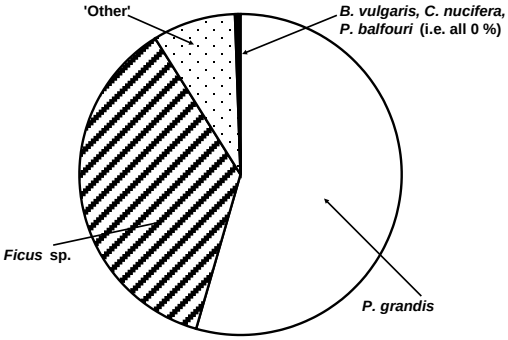
Fig. 3.3 Mean percentage ± SD of millipedes displaying the walking (*white bar*) and feeding (*dotted bar*) behaviours in 2003 in the Bamboo (n = 6); Coconut (n = 6) and Natural Forest (n = 6) study sites. Mann-Whitney U Test significant levels between the three sites for each behaviour type provided



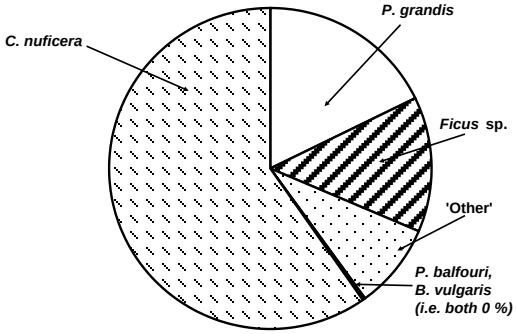
(ai) SGM leaf litter selection: Bamboo site



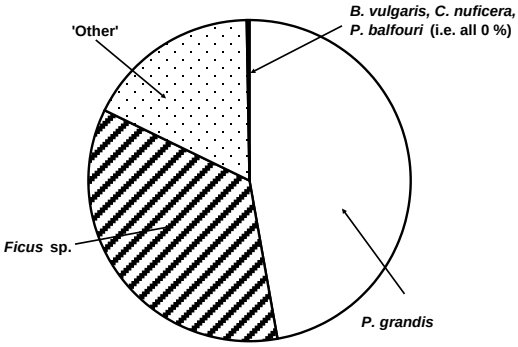
(aii) Leaf litter composition: Bamboo site



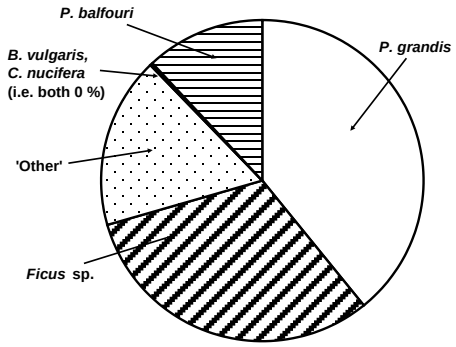
(bi) SGM leaf litter selection: Coconut site



(bii) Leaf litter composition: Coconut site



(ci) SGM leaf litter selection: Natural Forest site



(cii) Leaf litter composition: Natural Forest site

Fig. 3.4 (i) Percentage of millipedes feeding on *Pisonia grandis*, *Ficus* sp., *Pandanus balfouri*, *Bambusa vulgaris*, *Cocos nucifera* and 'Other' leaf litter types in the Bamboo (a), Coconut (b) and Natural Forest (c) study sites. **(ii).** Percentage leaf litter composition in the Bamboo (a), Coconut (b) and Natural Forest (c) study sites

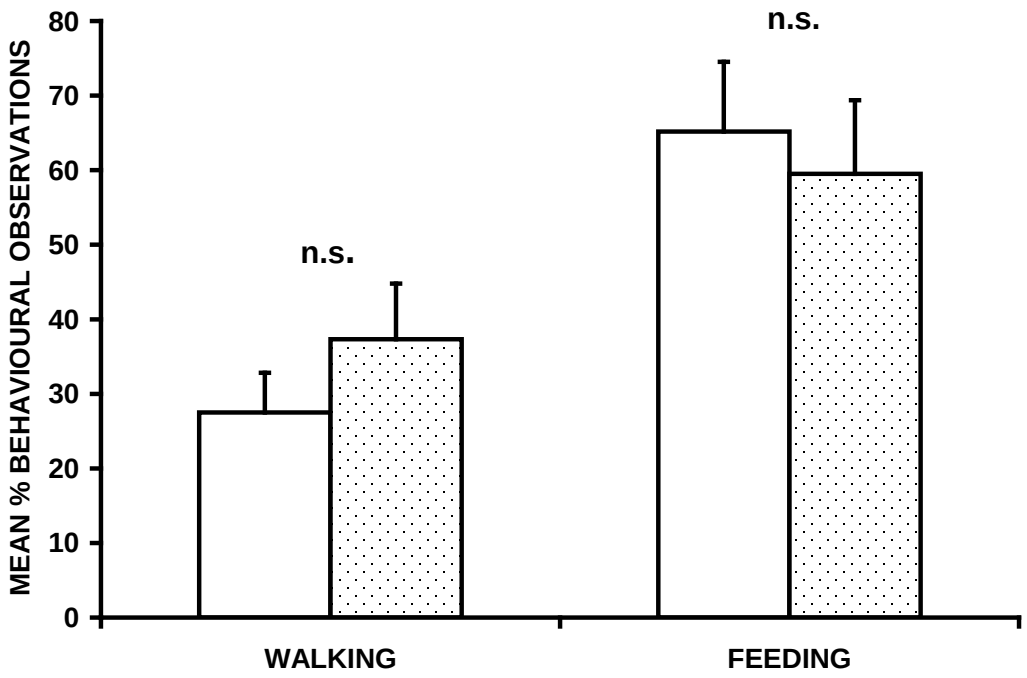


Fig. 3.5 Mean percentage ± SD of millipedes displaying the walking (n = 12) and feeding (n = 12) behaviours in the Bamboo study site in 2003 (*white bar)* and 2009 (*dotted bar*). Mann-Whitney U significance levels provided; n.s. not significant

CHAPTER 4

Response of a threatened giant millipede to forest restoration

Abstract

Understanding the response of threatened and functionally important island invertebrate species to plant community restoration is essential for the successful conservation of these invertebrate species. The Seychelles giant millipede (SGM), *Sechelleptus seychellarum*, is a threatened and functionally important macro-detritivore endemic to the Seychelles granitic islands. Here, I studied the response of this species to the ongoing forest restoration programme on Cousine Island, Seychelles. This study was conducted over an 11 year period, representing the floral succession of a formerly degraded open scrubland area, dominated by alien plants, to a closed canopy forest, dominated by planted indigenous trees. While the time span of this study was insufficient for vegetation height in the restored area to equal that in the reference natural forest, canopy closure was nevertheless comparable. I found SGM density to be an order of magnitude lower in the restored site compared to the natural forest. In contrast, SGM physical condition improved significantly in the restored site, as vegetation structure increased. Furthermore, SGM behaviour in the restored site switched from a predominantly walking to a predominantly feeding behaviour over the study period, resulting in the forest restoration programme on Cousine increasing the foraging area of the SGM by 43%. Competition for key resources, e.g. food and day-time refuges, are suggested as possible factors limiting SGM numbers in the restored forest.

Keywords: Cousine Island; density; detritivore; millipede; physical condition

4.1. Introduction

Islands worldwide are losing indigenous biodiversity from various, often synergistic, impacts (Walker and Bellingham 2011). Seychelles invertebrate biodiversity, with its high levels of endemism (Gerlach 2008a),

is primarily threatened by habitat deterioration as a result of historical deforestation and alien flora (Gerlach 2008b). As < 5 % of the original vegetation remains in the granitic Seychelles (Baider et al. 2010), forest restoration can potentially play an important role in reversing these impacts.

However, it has frequently been assumed that animals will colonise restored sites from surrounding areas as the succession of vegetation proceeds (Majer 2009). However, even where physiognomy and species composition of replanted vegetation successfully emulates that of an undisturbed reference site, the colonisation by native fauna is not always guaranteed. Although for many forest invertebrates, including soil-dwelling species, creating a forest-like structure is important in catalysing their rapid colonisation of restored areas (Grimbacher and Catterall 2007; Nakamura et al. 2009), very little is known about their response to changes in vegetation structure.

Here, I focus on the Seychelles giant millipede (SGM), *Sechelleptus seychellarum* (Desjardins 1834) (Diplopoda: Spirostreptida: Spirostreptidae), as it is a very large (up to 240 mm in length) and abundant, or formerly abundant, macro-detritivore endemic to the Seychelles granitic islands (Golovatch and Gerlach 2010). The SGM is IUCN Red Listed as “Vulnerable” (IUCN 2011) making it a notable conservation subject. Furthermore, many tropical millipedes, including the SGM (Lawrence and Samways 2003), play a significant role in litter breakdown and nutrient dynamics (Reddy 1995), making their colonisation of restored sites potentially important for restoring ecosystem functions (Snyder and Hendrix 2008).

As many threatened invertebrates depend on some form of habitat restoration, which is generally vegetation-based (New 2009), determining whether forest restoration practices would create suitable habitat for the SGM is important for the success of such efforts, and for its own conservation. This study was conducted over an 11 year period on Cousine Island, Seychelles, representing the floral succession of a degraded open scrubland area, dominated by alien plants, to a closed canopy forest, dominated by planted indigenous trees. The objective of this study was to compare temporal and spatial patterns of *S. seychellarum* population density, physical condition and behavioural attributes in a newly restored site to those attributes in an adjacent natural site. As the SGM is primarily associated with a forest biotope (Lawrence 1999), I predicted that as the vegetation structure of the restored area became comparable to the native forest, this millipede would successfully colonise the restored forest, with the focal attributes approaching those in the indigenous forest.

4.2. Methods

4.2.1. Study site

Cousine Island is a small granitic island (4° 20' 4" S and 55° 38' 44" E) (Fig. 4.1a) that is 27 ha, ± 1 km long, 400 m wide with a maximum elevation of 65 m. Cousine falls within a biodiversity hotspot (Myers et

al. 2000), and is considered a 'Key Biodiversity Area' within Seychelles (Gerlach 2008a). Moreover, it is apparently the only tropical island >20 ha globally which has never had any mammal invasions (Samways 2000). Cousine has undergone much restoration in terms of alien plant species and domestic livestock removal, with forest restoration also having taken place (Samways et al. 2010).

The vegetation (Fig. 4.1b) is mostly forest areas (14 ha) dominated by indigenous *Euphorbia pyrifolia* Lam., *Ficus reflexa* Thunb., *F. lutea* Val., *Pisonia grandis* R.Br. and *Pandanus balfouri* Mart. trees. A coastal plain (6 ha) was previously used for agriculture and livestock farming. Forest probably occupied the coastal plain, a historical condition to which it has been restored by high density planting of indigenous saplings (Samways et al. 2010). A small, demarcated agricultural area (1 ha) is situated in the centre of the island, and is dominated by mowed *Cynodon dactylon* (L.) Pers. grass. The remaining 6 ha consisted of natural grassland and herb areas.

The natural forest and restoration areas formed the two main study sites. For analysis, data from both natural forest areas were combined. Since all sites lie adjacent to each other, the effect of site isolation, which often influences invertebrate colonization of restored areas (Knop et al. 2011), was eliminated.

The Seychelles islands experience a tropical climate and, although considered non-seasonal, the summer NW monsoon (i.e. October to April) brings higher rainfall than the winter SE trade winds (i.e. May to September). All data were collected during the wet NW monsoon, as millipede surface activity was highest during this period (Chapter 2). Data were collected during six survey periods between 1998 and 2009: February 1998 – April 1998; October 2002 – November 2002; February 2003 – April 2003; October 2005; February 2007 – March 2007; April 2009.

4.2.2. Vegetation structure and millipede density

Vegetation structure and millipede density were determined using 1×10 m transects. The position of transects were chosen to cover as much of the island as possible. For the 1998 (n = 160) survey, the starting point of each transect was randomly selected in areas of different dominant vegetation type. Using GPS, each transect was begun at the intersection point of a hypothetical 50×50 m grid overlay for the 2002 (n = 52), 2003 (n = 140), 2005 (n = 50), 2007 (n = 50) and 2009 (n = 52) surveys. The total number of transects over the 11 year study period was 504. Data were subdivided into the two sites for analyses.

As the SGM is primarily nocturnal, millipede density was determined between 20:00 and 22:30 by counting the number of individuals per transect. A total of 15154 millipede individuals were sampled over the 11 year period. As millipede density fluctuated throughout the study period (Chapter 2), the percentage mean millipede density in the restoration site relative to the mean millipede density in the natural forest was calculated.

Vegetation structure, determined during the day at the centre point of each transect, was calculated as the change in canopy closure and vegetation height. Canopy closure was visually estimated to the nearest

10 %. Vegetation height was visually estimated in metres and was ranked as follows for data analysis: 1 = vegetation < 2.0 m; 2 = vegetation between 2.1 – 5.0 m; 3 = vegetation > 5.0 m.

4.2.3. SGM physical condition and behaviour

SGM physical condition assessments and behavioural observations were made at night between 20:00 and 22:30 in each survey year. The physical condition and behaviour of randomly sampled SGM individuals in the natural forest and restoration sites were recorded. Where millipede density was high, a 0.25 m^2 quadrat was used to randomly select individuals.

To determine SGM physical condition, each sampled individual was assigned an activity rating after being disturbed: 1 = individual dead; 2 = individual alive, but not moving; 3 = individual sluggish in movement; 4 = individual showing some walking activity; 5 = individual very actively walking. A mean activity rating was calculated for each site per survey year. Four-hundred SGM individuals were sampled per survey period, with the total sample size over the 11 year period being 2400 millipedes.

Six main behavioural types were displayed by the SGM: walking, feeding, copulating, resting, burrowing and grooming. The dominant behaviours were walking and feeding (Lawrence and Samways 2003). Walking was assumed to be associated with the search for suitable conditions and resources such as food or potential mates. Feeding consisted of individuals ingesting food items such as bark, sticks, fallen fruit, bird faeces, soil/algae, flowers, with leaf litter making up the largest percentage (i.e. ± 55 %) of all feeding observations (Lawrence and Samways 2003). As the other four behaviour types were rarely observed their results are only briefly reported on in this study.

SGM individuals were sampled over six nights per survey year. The mean percentage of SGM individuals displaying the walking and feeding behaviour types relative to the total number of behaviour observations (i.e. for all six behaviour types) per survey period in both sites was calculated. A total of 3231 walking and feeding millipede observations were made over the 11 years i.e. 1998 (n = 1188), 2002 (n = 134), 2003 (n = 1029), 2005 (n = 205), 2007 (n = 436) and 2009 (n = 239).

4.2.4. Statistical analyses

All statistical analyses were carried out using STATISTIXL 1.8 (2007) software. Non-parametric inferential tests were used as data did not satisfy parametric assumptions (Siegel and Castellan 1988). Kruskal-Wallis tests were used to test for any significant differences in vegetation height, percentage canopy closure, millipede activity, and percentage behaviour over the 11 year study period. A Spearman rank correlation r_s test was used to assess for any significant correlation in percentage mean millipede density and time in the restoration site. Mann-Whitney U tests were used to test for any significant differences between mean: vegetation height and percentage canopy closure in 1998 and 2009; activity

ratings of SGM individuals in the forest and restoration sites from 1998 to 2009; percentage of individuals displaying each behaviour type in the forest and restoration sites from 1998 to 2009.

4.3. Results

4.3.1. Vegetation structure

Vegetation height (range: 2.70 to 2.84; Kruskal-Wallis Test, n.s.; n = 380) and percentage canopy closure (range: 62.50% to 69.50%; Kruskal-Wallis Test, n.s.; n = 380) in the natural forest remained stable over the study period (Fig. 4.2). Both vegetation height (Kruskal-Wallis Tests, $P < 0.001$; n = 124) and percentage canopy closure (Kruskal-Wallis Test, $P < 0.001$; n = 124) increased significantly from 1998 to 2009 in the restoration site. Here, mean ± SD vegetation height (Mann-Whitney U Test, $P < 0.01$) and mean ± SD percentage canopy closure (Mann-Whitney U Test, $P < 0.001$) increased significantly from 1.28 ± 0.64 (n = 40) and 7.00 ± 1.74% (n = 40) respectively in 1998, to 2.00 ± 0.66 (n = 12) and 71.67 ± 2.67% (n = 12) respectively in 2009.

4.3.2. SGM density

SGM density was an order of magnitude higher in the natural forest compared with the restoration site in each survey year (n = 504). The mean percentage density in the restoration site increased over the 11 year period (Fig. 4.3), although this increase was not significant (Spearman $r_s = 0.633$, n.s. n = 6).

4.3.3. SGM physical condition

Mean activity remained unchanged in the natural forest site over the study period (range: 4.71 to 4.86; Kruskal-Wallis Test, n.s. n = 2400). In the restoration site, activity increased significantly from a mean ± SD of 4.27 ± 1.31 (n = 200) in 1998 to a mean ± SD of 4.68 ± 0.93 (n = 200) in 2009 (Mann-Whitney U Test, $P < 0.01$).

In 1998 (n = 400), 2002 (n = 400), 2003 (n = 400) and 2005 (n = 400) mean activity was significantly higher in the natural forest than in the restoration site (Mann-Whitney U Tests; see Fig. 4.4 for *P* values). In 2007 (n = 400) and 2009 (n = 400) there were no significant differences between the mean activity of SGM individuals in the natural forest and restoration sites (Mann-Whitney U Tests; see Fig. 4.4 for *P* values).

4.3.4. SGM behaviour

The percentage of SGM individuals displaying the walking (range: 6.50% to 15.17%; Kruskal-Wallis Test, n.s.; n = 36; Fig. 4.5a) and feeding (range: 67.28% to 78.67%; Kruskal-Wallis Test, n.s.; n = 36; Fig. 4.5b) behaviours remained stable throughout the study period in the natural forest site.

In the restoration site, the percentage of SGM individuals displaying the walking behaviour decreased significantly from 65.67 ± 4.18% (n = 6) in 1998 to 24.83 ± 1.83% (n = 6) in 2007 (Mann-Whitney U Test, $P < 0.001$), with the greatest decrease occurring between 2005 and 2007. The percentage of SGM individuals displaying the feeding behaviour in the restoration site increased significantly from 13.17 ± 2.79% (n = 6) in 1998 to 61.17 ± 4.38% (n = 6) in 2007 (Mann-Whitney U Test, $P < 0.001$), with the largest increase occurring between 2005 and 2007.

The walking behaviour was more commonly observed in the restoration site than the natural forest site in each survey year (Mann-Whitney U Tests; n = 72; see Fig. 4.5a for *P* values). The feeding behaviour was more often observed in the natural forest site than the restoration site in each survey year (Mann-Whitney U Tests; n = 72; see Fig 4.5b for *P* values).

The other four behaviour types were rarely sampled. In the natural forest and restoration sites these other behaviours comprised the following percentage of the observations respectively: Copulating = 0.27 % / 0.00 %; Resting = 1.34 % / 3.46 %; Burrowing = 3.97 % / 0.92 %; Grooming = 3.11 % / 1.55 %. The results represent combined data for all survey periods.

4.4. Discussion

Seychelles giant millipede (SGM) density was an order of magnitude lower in the restored area than in the natural forest, despite the vegetation structure in the restored site converging towards that of the natural forest. Furthermore, although not statistically significant, millipede densities in the restored forest showed a slight increase over the study period. However, the SGM did nevertheless respond positively to the increase in vegetation structure by showing a significant improvement in physical condition and increased foraging activity as vegetation succession proceeded in the restoration site.

While the time span of this study was insufficient for the vegetation height in the restored area to equal that of the natural forest, canopy closure was comparable by 2007. A closed forest canopy is considered important for ground-dwelling invertebrates (Nakamura et al. 2009). Certainly here, SGM physical condition improved in the restored site over the 11 year period. An increase in forest canopy closure created a shaded forest floor with an increase in leaf litter (Lawrence 2009). This results in cooler micro-climatic conditions (Sayer 2005), which are beneficial for millipedes (Hopkin and Read 1992).

Furthermore, SGM behaviour in the restored site switched from a predominantly walking to a predominantly feeding behaviour over the study period. The improved micro-climatic conditions, with an

increase in potential food source, would allow the SGM to spend more time feeding and less time searching for suitable food items. This change in vegetation structure in the restoration site increased the SGM foraging area by 43% from 14 ha to 20 ha.

The direct effect of vegetation height on forest floor invertebrates is less clear, and is possibly more important for aerial invertebrates, as it was found to be a significant predictor of the occurrence of flying beetles in replanted rainforests plots (Grimbacher and Catterall 2007).

So what prevented the SGM from successfully colonising the restored site in similar densities to those in the natural forest? Here, I discuss five potential factors which could explain the observed results: dispersal ability; leaf litter quality; the impact of invasive species; restoration site age; and resource quantity and availability.

Dispersal ability: Dispersal ability is a fundamental factor influencing invertebrate colonisation of created habitats (Moir et al. 2005). Invertebrate dispersal ability often goes hand in hand with the degree of isolation of a restoration site, with outlying sites showing reduced colonisation success (Nakamura et al. 2008). In this study, the restored site was adjacent to the natural forest site. Although millipedes generally have a limited dispersal capacity (Hopkin and Read 1992), mark-resighting observation carried out in the forested areas on Cousine found the SGM to be mobile, with individuals regularly travelling > 20 m, and some individuals travelling > 60 m, within 24 hr (J. Lawrence unpubl. data). These distances would easily allow millipedes to colonise the restored site, making poor dispersal ability an unlikely factor.

Leaf litter quality: Certain millipede species have been shown to prefer feeding on leaf litter rich in nitrogen, with a low C:N ratio (Kadamannaya and Sridhar 2009). Leaf litter quality can influence the spatial biomass of some species (Warren and Zou 2002). However, leaf litter quality was not considered to be a factor here for two reasons: 1) SGM feeding observations increased as the vegetation structure increased in the restored site; 2) many indigenous forest tree species were planted in the restored site as part of the restoration programme (Samways et al. 2010), suggesting similar quality leaf litter was available in both sites.

Invasive species impact: The impact of invasive species on island fauna can be of major local consequence. One species that is of particular interest on Cousine is the invasive African big-headed ant, *Pheidole megacephala* (Fabricius), which is abundant in parts of the restored area, as well as other areas on the island, where it has displaced many indigenous invertebrates (Gaigher et al. 2011). However, the defence secretions of the SGM successfully protected it from *P. megacephala* predatory attacks, and both ant and millipede spatial distributions overlapped in areas where the ant was abundant (Lawrence et al. 2011).

Restoration site age: The influence of site age on invertebrate colonisation of restored areas is varied. For example, Ramalingam and Rajan (2009) found that the diversity of ground insect assemblages was correlated with site age trajectory. Other studies found invertebrates to respond to the structure, rather than the age *per se*, of regenerating areas (e.g. Nakamura et al. 2003). However, for the SGM, a more

suitable habitat could possibly be created as the vegetation begins to establish in the restored area on Cousine.

Resource quantity and availability: The low density of the SGM in the restored forest suggests that competition for key resources could be a limiting factor. Two possible resources are food (i.e. leaf litter) quantity and day-time refuge availability. SGM individuals have been observed occupying granitic rock crevices during daylight hours (Gerlach et al. 2005), suggesting they may form necessary habitat components for this species. Furthermore, logs were found to form important habitats elements for many Seychelles forest-floor arthropods (Kelly and Samways 2003). However, the potential effects of the quantity and availability of these resources as factors limiting SGM density in the restored forest would require further testing.

Understanding the response of threatened and functionally important invertebrates to restoration practices can be vital for the successful conservation of such species. This can be particularly important for endemic island invertebrates, which frequently have small population sizes, further limited by a lack of suitable habitat (New 2008). While the SGM has thus far failed to successfully colonize the restored site in large numbers here, the forest restoration programme did nevertheless benefit this species by providing more extensive foraging areas and improved conditions for it. This study clearly shows that a species' response to management activities, such as forest restoration, may not be clear-cut. While focussing on the population response is certainly more useful from a conservation perspective, understanding how such a management activity can influences a species' behaviour and physical condition can indicate that certain key resources may be limiting, thus assisting with understanding a target invertebrate's habitat requirements.

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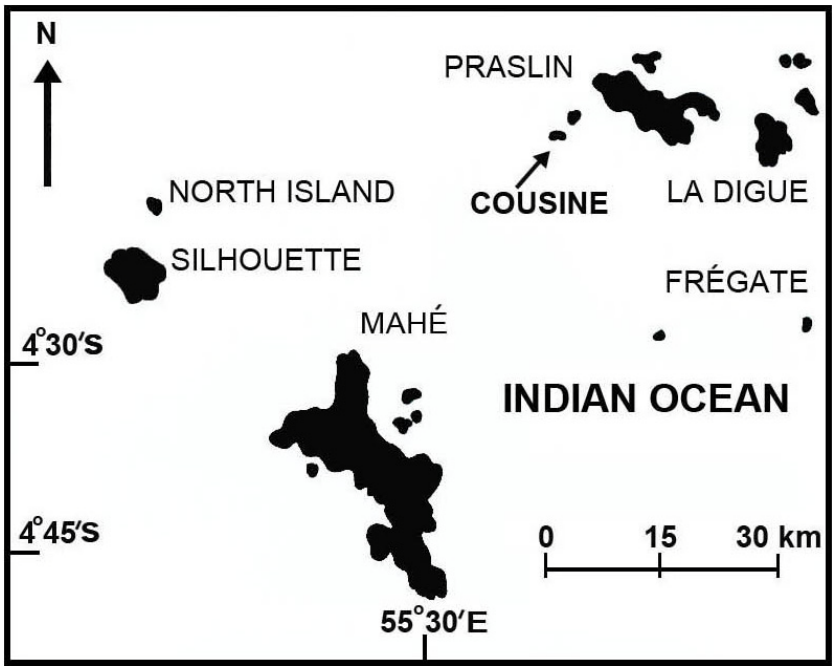
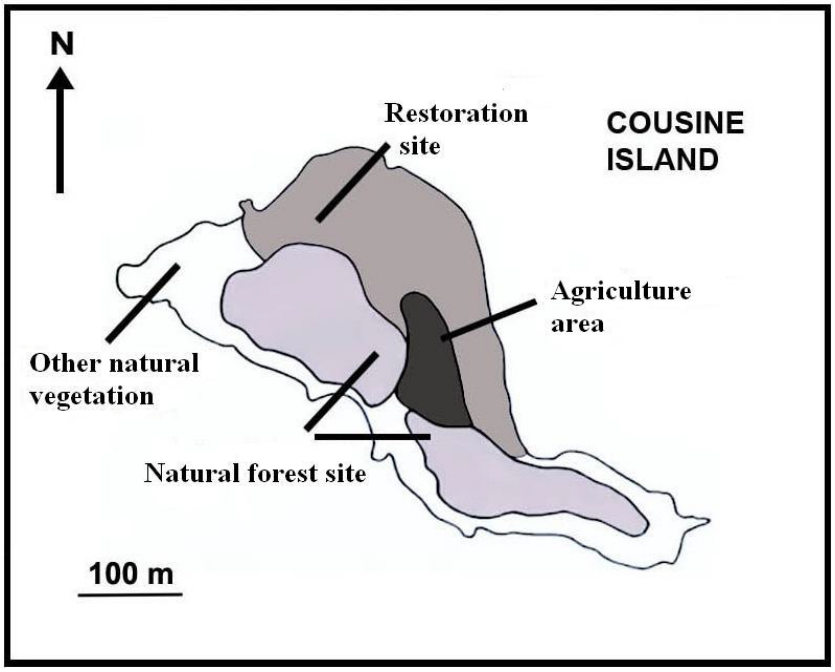
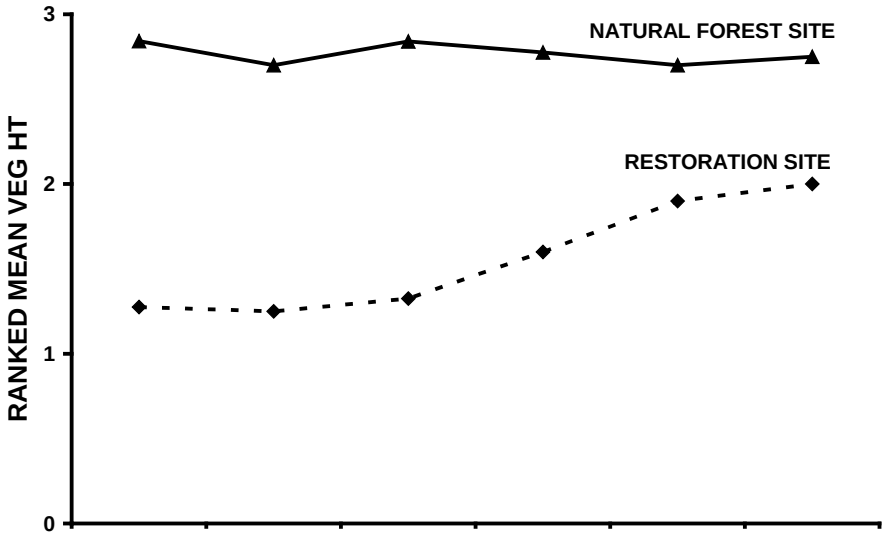


(a)

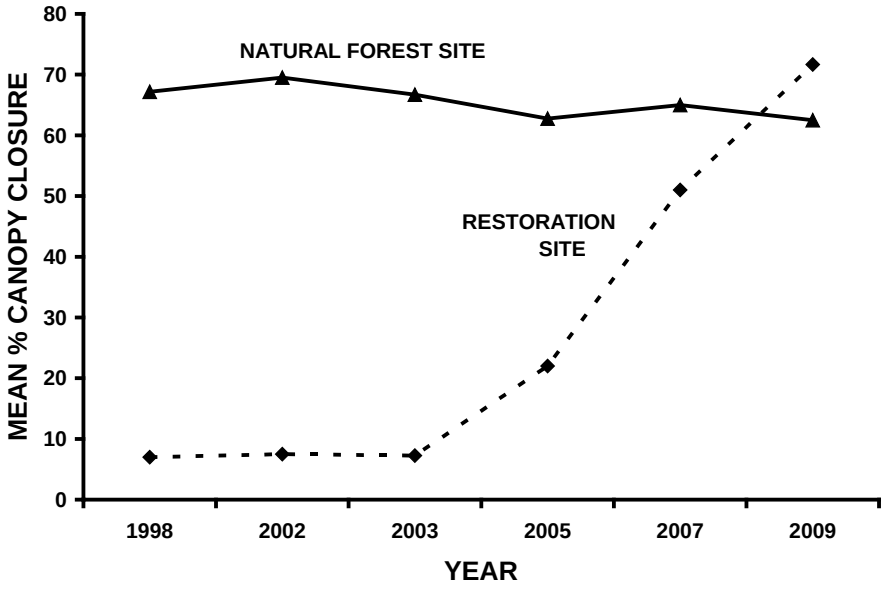


(b)

Fig. 4.1 a Central group of Seychelles granitic islands, showing the position of Cousine Island, Seychelles. **b** Simplified vegetation types of Cousine Island, Seychelles, showing the position of the two study sites. 'Other natural vegetation' and the agricultural areas were not used in this study



(a)



(b)

Fig. 4.2 a Ranked mean vegetation height in the natural forest (n = 380) and restoration (n = 124) sites between 1998 and 2009 on Cousine Island, Seychelles. Vegetation height was ranked as follows: 1 = vegetation < 2.0 m; 2 = vegetation between 2.1 – 5.0 m; 3 = vegetation > 5.0 m. **b** Mean percentage canopy closure visually estimated to the nearest 10% in the natural forest (n = 380) and restoration (n = 124) sites between 1998 and 2009 on Cousine Island, Seychelles

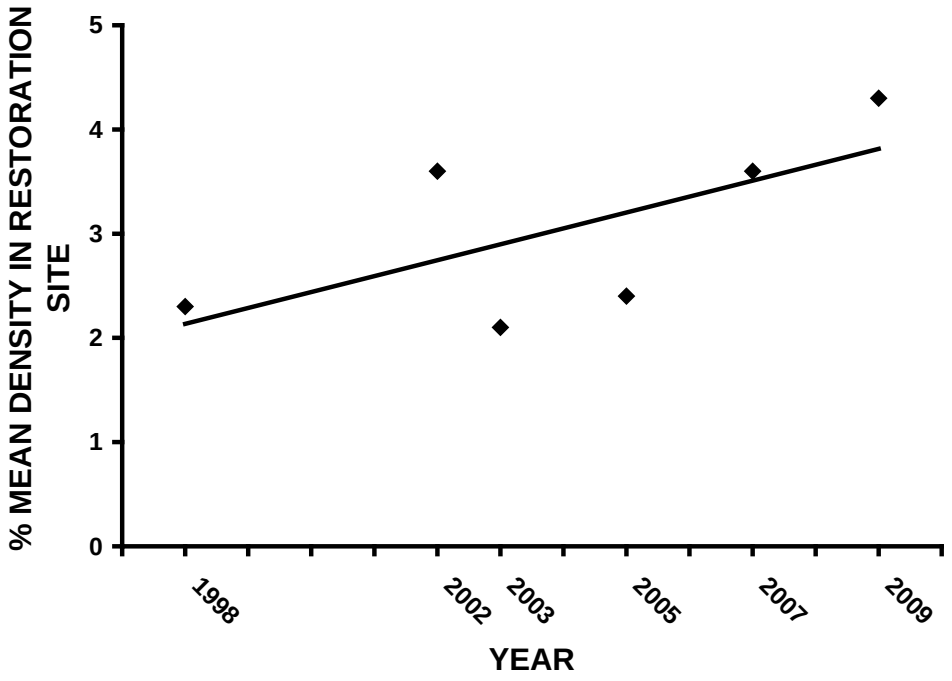


Fig. 4.3 Percentage mean millipede density per 1 m × 10 m transect between 1998 and 2009 in the restoration site relative to the natural forest areas on Cousine Island, Seychelles

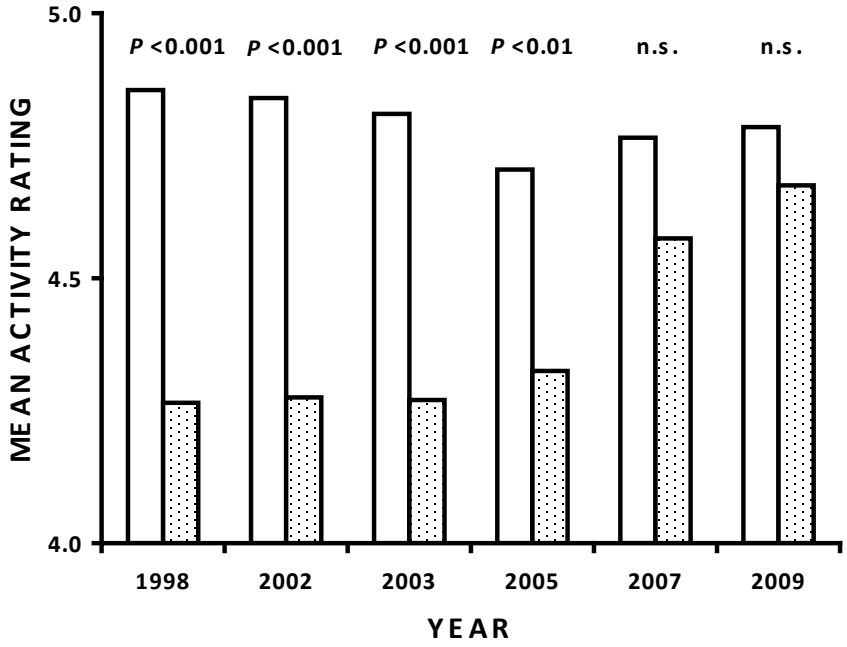
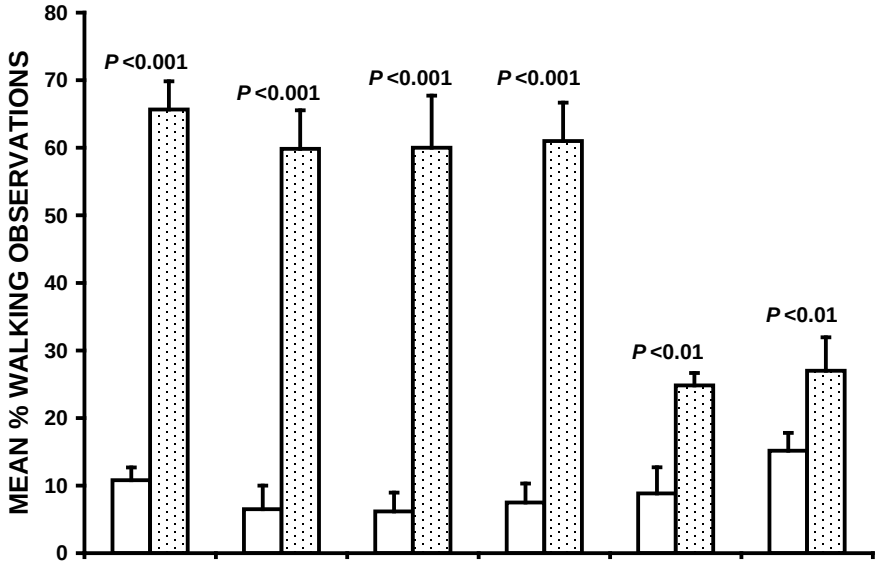
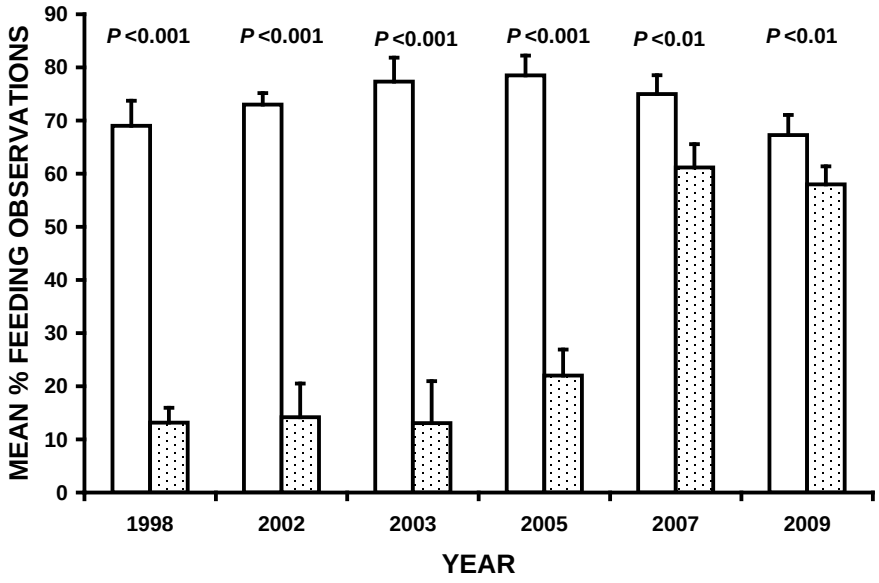


Fig. 4.4 Mean activity rating of millipedes in the natural forest (*white bar*; n = 1200) and restoration (*dotted bar*; n = 1200) sites in each survey year on Cousine Island, Seychelles. Mann-Whitney U Test significance levels between each site per survey year provided. NOTE: y-axis value begins at 4.0



(a)



(b)

Fig. 4.5 Mean percentage ± SD of millipedes displaying the **(a)** walking and **(b)** feeding behaviours in the natural forest (*white bar*; n = 36) and restoration (*dotted* bar; n = 36) sites in each survey year on Cousine Island, Seychelles. Mann-Whitney U Test significance levels between each site per survey year provided

CHAPTER 5

Beyond vegetation-based habitat restoration for a threatened giant Spirostreptid millipede

Abstract

Vegetation-based restoration efforts often fail to provide suitable habitat for many invertebrates. Restoring habitat for target invertebrates requires an understanding of their resource and condition requirements. The Seychelles giant millipede (SGM), *Sechelleptus seychellarum*, is a functionally important millipede which is Red Listed as "Vulnerable". Here, I studied the habitat requirements of this macro-detritivore in relation to the ongoing forest restoration programme on Cousine Island, Seychelles. SGM spatial density did not significantly correlate with edaphic and litter properties, but did positively correlate with the toposcape (i.e. elevation and granitic rock cover). Granite rock crevices in forest covered areas were important diurnal refuges for the SGM, as microclimate conditions in non-forest covered rock refuges were unsuitable. SGM physical condition was significantly lower in non-shaded crevices compared to those shaded by forest. Low granite rock cover in the restored forest limited the SGM colonisation of this area in large numbers, despite canopy cover in the restored forest being comparable with that in the reference natural forest. As most restoration practices are primarily vegetation-based, this study demonstrates that such an approach can be inadequate for restoring habitat for target invertebrates, as many species habitat requirements extend beyond that of vegetation. For the SGM, selecting restoration sites that already have abundant rock cover would be the most practical way to increase SGM habitat through forest restoration practices. Taking into consideration the habitat requirements of target invertebrates can help in setting or redirecting restoration goals and thus enhance the conservation value of such practices.

Keywords microclimate; resource; rock refuges; *Sechelleptus seychellarum*; site selection; spatial density

5.1. Introduction

The loss and degradation of habitat is recognised as the greatest threat to invertebrate biodiversity (Samways et al. 2010a). Efforts to restore degraded areas for terrestrial invertebrates are often vegetation-based (New 2009), and frequently assume animals will colonise these sites from surrounding areas as the succession of vegetation proceeds (Majer 2009). However, studies that have addressed invertebrate colonisation of vegetation-based restoration sites often reveal poorer species diversity or lower abundance in these restoring/restored sites. As invertebrates are key players in ecosystem processes, understanding the habitat requirements of target species, e.g. threatened, functionally important or umbrella taxa (Karjalainen 2005), can help direct or set restoration goals to take into account the requirements of these species and so improve the overall conservation value of these efforts.

Although for many forest invertebrates, including soil species, creating a forest-like vegetation structure is important in catalysing their rapid colonisation of restored areas (Grimbacher and Catterall 2007; Nakamura et al. 2009), both biotic and abiotic factors influence millipede distributions (Golovatch and Kime 2009). Here, I focus on the Seychelles giant millipede (SGM), *Sechelleptus seychellarum* (Desjardins) (Diplopoda: Spirostreptida: Spirostreptidae) as it is charismatic (up to 240 mm in length), IUCN Red Listed as "Vulnerable" (IUCN 2011) and endemic to the Seychelles granitic islands (Golovatch and Gerlach 2010), making it a notable conservation subject. Furthermore, many tropical millipedes, including the SGM (Lawrence and Samways 2003), play a significant role in litter breakdown and nutrient dynamics (Reddy 1995), making their colonisation of restored sites potentially valuable for restoring ecosystem processes (Snyder and Hendrix 2008).

Although the SGM is extirpated on several islands, it is still common on Cousine Island, Seychelles (Lawrence 1999). Cousine falls within a biodiversity hotspot (Myers et al. 2000) and is considered a 'Key Biodiversity Area' within Seychelles (Gerlach 2008). Furthermore, it is apparently the only tropical island globally >20 ha which has never had any mammal invasions (Samways 2000). Cousine has undergone much restoration in terms of alien plant species and domestic livestock removal, with forest restoration also having taken place (Samways et al. 2010b). Despite the SGM being primarily associated with a forest biotope (Lawrence 1999), individuals did not colonise the restored forest on Cousine in similar high densities to those in the natural forest, even though the restored forest provided suitable foraging areas and improved conditions for this species (Lawrence et al. 2012). As successful conservation focuses on populations, understanding what limited SGM densities in the restored forest is considered important for the success of Seychelles forest restoration efforts and for the millipedes' own conservation.

Subsequently, this study aims to identify which surface habitat elements are key resources limiting SGM densities in the restored forest on Cousine Island, Seychelles. Soil and litter arthropods, including millipedes, are sensitive to desiccation (Hopkin and Read 1992) and many surface elements. Edaphic properties (Kime and Golovatch 2000), litter material (David and Handa 2010; Evans et al. 2003), the toposcape (Golovatch and Kime 2009; Samways 1994), and microclimate conditions (Berġholz 2007) are

considered potentially significant surface elements. Spatial heterogeneity in surface elements across Cousine was expected to influence SGM spatial density on the island, and thus the suitability of the restored forest as habitat for the millipede. Recommendations are then made that can be used to re-direct or set certain restoration goals to take into account the specific habitat requirements of this threatened and functionally important species.

5.2. Methods

5.2.1. Study site

Cousine Island is a small granitic island (4° 20' 4" S and 55° 38' 44" E) (Fig. 5.1a) that is just over 1 km long, 400 m at its widest point, covers 27 ha, consists of a hill and ridge separated by a saddle, and a coastal plain on the northern and eastern sides of the island (Fig. 5.1b).

The hill and ridge vegetation comprises mostly natural forest (14 ha) dominated by indigenous *Euphorbia pyrifolia* Lam., *Ficus reflexa* Thunb., *F. lutea* Val., *Pisonia grandis* R.Br. and *Pandanus balfouri* Mart. trees. A coastal plain (6 ha) was previously used for agriculture and livestock farming. Forest probably originally occupied the coastal plain, a historical condition to which it has been restored by high density planting of indigenous saplings (Samways et al. 2010b). At the time this study was conducted, vegetation height in the restored area was lower than in the reference natural forest, but canopy closure was comparable, with a closed canopy forest attained by 2007 (Lawrence et al. 2012). A demarcated agricultural area (1 ha) is situated in the centre saddle of the island, and is dominated by mowed *Cynodon dactylon* (L.) Pers. grass. The remaining 6 ha consists of low-lying coastal natural grassland and herb areas (Fig. 5.1b).

5.2.2. Surface habitat elements and millipede spatial density

A number of edaphic, litter and toposcape habitat elements that could potentially influence SGM spatial density on Cousine are summarised in Table 5.1. Sixty 1 m × 10 m transects were walked between February and March 2007. The position of transects were chosen to cover as much of the forested area on the island as possible, including the restored area. As all transects were confined to areas >60% canopy closure, no data were collected in the agricultural and natural grassland/herbland areas.

Millipede density was determined at night between 20:00 and 22:30 by counting the number of individuals active on the forest-floor per transect. Soil moisture, soil pH, soil depth, leaf litter cover and transect elevation were quantified during the day using a 0.25 m^2 square quadrat placed at a suitable non-rock covered point along each transect. Furthermore, the percentages of granite rock cover and wood debris density per transect were also determined. Granite rocks were defined as a rock or rock pile $\geq$0.25 m^2.

Following Kelly and Samways (2003), wood debris was defined as logs having a diameter≥0.1 m and length ≥0.5 m.

5.2.3. Millipede response to granite rock areas

Data were collected April - May 2009 in forest covered and non-forest covered areas on the island that had abundant granite rock cover. Rocks in the forest covered areas were sheltered from direct sunlight by >60% canopy cover. Rocks in the non-forest covered areas were exposed to direct sunlight for most of the day. Data were collected between 11:30 – 13:30 and 20:30 – 22:30, except for the physical condition data (see below), which was only collected during daylight hours. Furthermore, data were collected when the wind was calm and cloud cover was 0%.

To estimate millipede density in rocky areas, 1 m^2 rocky quadrats and adjacent 1 m^2 bare quadrats were thoroughly searched, including all accessible rock crevices where applicable, for millipedes and the number of individuals counted. Adjacent bare quadrats were randomly selected 1 m from rocky quadrats. Rocky quadrats had >90% rock cover. Bare quadrats had 0% rock cover. Forty rocky/bare quadrat pairs were selected in forested areas (i.e. 20 during the day and 20 at night) and 40 selected in non-forested areas (i.e. 20 during the day and 20 at night).

All microclimate data were collected on four days/nights in April 2009 using an Extech Hygro-Thermometer. The % Relative Humidity (RH) and temperature (°C) in rock crevices and adjacent bare ground spot points, randomly selected 1 m from the rock crevice were recorded. Forty rock crevice/bare ground spot point pairs were selected in forested areas (i.e. 20 during the day and 20 at night) and 40 selected in non-forested areas (i.e. 20 during the day and 20 at night).

Suitable rock crevices were identified during the day by the presence of≥1 millipede, and the rock crevice marked for later night-time identification. Diurnal and nocturnal RH and temperature readings were recorded from the same rock crevice. All SGM individuals were removed from rock crevices before microclimate readings were taken. The physical condition of removed millipedes was determined by assigning an activity rating: 1) millipede dead; 2) millipede alive, but sluggish; 3) millipede active.

The vapour pressure deficit (VPD) was calculated from the % RH and temperature T (º C) readings using the following formula (Monteith and Unsworth 2008; Murray 1967):

$$\text{Vapour pressure deficit (Pa)} = (100 - RH / 100) \times (610.7 \times 10^{(7.5 \times T) / (237.3 + T)})$$

VPD is a convenient measure of the drying power of the air (Rosenberg 1974), and the rate of evaporative water loss from an invertebrate is proportional to the VPD (Holmstrup et al. 2010), with high VPDs considered unsuitable for the SGM.

5.2.4. Statistical analyses

All statistical analyses were carried out using STASTISTIXL 1.8 (2007) software. Non-parametric inferential tests were used as data did not satisfy parametric assumptions (Siegel and Castellan 1988). Spearman Rank Correlation tests were used to test for any significant correlations between millipede density and surface elements. Kruskal-Wallis and Mann-Whitney U Tests were used to test for any significant differences in millipede density and percentage rock cover in the forested areas on the North hill, South ridge and Coastal plain. Mann-Whitney U Tests were performed between: mean millipede density in bare and rocky quadrats; mean activity rating of millipedes from forest covered and non-forest covered rock crevices; mean VPD in rock crevice and bare ground spot points.

5.3. Results

5.3.1. Surface habitat elements and millipede spatial density

Spearman Rank Correlations between millipede density and the various surface habitat elements are shown in Fig. 5.2. Significant positive correlations were found between millipede spatial density and toposcape habitat elements (Table 5.2) i.e. percentage granite rock cover (r_s = 0.855; Spearman Rank Correlation; P<0.001, n = 60) and elevation (r_s = 0.617; Spearman Rank Correlation; P<0.001, n = 60). Furthermore, there was a significant positive correlation between percentage rock cover and elevation (r_s = 0.614; Spearman Rank Correlation; P< 0.001, n = 60). No significant correlations were found between millipede spatial density and edaphic or litter material elements (Spearman Rank Correlations; all n.s.).

5.3.2. Spatial relationship between millipede and rock cover

Millipede individuals were significantly more numerous on the North hill (Mean ± SD: 3.14 ± 1.71 ind.m^{-2}; n = 20) and South ridge (Mean ± SD: 1.91 ± 1.12 ind.m^{-2}; n = 20), compared to the Coastal plain (Mean ± SD: 0.11 ± 0.08 ind.m^{-2}; n = 20) (Kruskal-Wallis and Mann-Whitney U Tests, all P < 0.001). Mean rock cover was significantly higher on the North hill (Mean ± SD: 41.3 ± 19.9%; n = 20) and South ridge (Mean ± SD: 39.0 ± 19.4 %; n = 20) than on the Coastal plain (Mean ± SD: 5.0 ± 5.1%; n = 20) (Kruskal-Wallis and Mann-Whitney U Tests, all P < 0.001) (Fig. 5.3).

5.3.3. Millipede density in rocky and non-rocky quadrats

Mean millipede densities were higher in forest covered 1 m^2 quadrats compared with non-forest covered 1 m^2 quadrats (Fig. 5.4). In the forest covered areas, millipede diurnal density in rocky 1 m^2 quadrats (Mean

± SD: 4.30 ± 1.84 ind.m^{-2}; n = 20) was significantly higher than in bare 1 m^2 quadrats (Mean ± SD: 0.15 ± 0.37 ind.m^{-2}; n = 20; Mann-Whitney U Test, $P < 0.001$). No significant differences were found between millipede nocturnal densities in rocky and bare 1 m^2 quadrats in both forest covered and non-forest covered areas (Mann-Whitney U Tests, both n.s.).

5.3.4. *Sechelleptus seychellarum* condition from rock crevices

Mean activity rating was significantly higher for millipedes sampled from forest covered rock crevices (Mean: 2.88 ± 0.43; n = 121) compared to those sampled from non-forest covered rock crevices (Mean: 1.10 ± 0.31; n = 40; Mann-Whitney U Test, $P < 0.001$).

5.3.5. Microclimate in rock crevices

Mean VPD was highest during the day in the non-forest covered area (Fig. 5.5). In the forest covered area, VPD was significantly lower during the day in rock crevices (Mean ± SD: 0.86 ± 0.50 KPa, n = 20) compared with bare ground spot points (Mean ± SD: 1.92 ± 0.48 KPa, n = 20; Mann-Whitney U Tests, $P < 0.001$). Importantly, in the forest covered area there was no significant difference between diurnal rock crevice VPD and nocturnal spot point VPD (Mann-Whitney U Test, n.s., n = 40). No significant differences were found between diurnal and nocturnal rock crevice and spot point VPDs in the non-forest covered area (Mann-Whitney U Tests, both n.s.), or between nocturnal rock crevice and bare ground spot point VPDs in the forest covered area (Mann-Whitney U Test, n.s., n = 40).

5.4. Discussion

Although the SGM mostly occurs in the forest covered areas on Cousine (Lawrence 1999), spatial density was nevertheless heterogeneous in these areas. Such small-scale heterogeneous distributions are not uncommon for millipedes (e.g. Dangerfield 1990). While both edaphic and litter elements can potentially influence millipede distributions, particularly at the landscape level (David and Handa 2010; Golovatch and Kime 2009; Kime and Golovatch 2000), they had little impact on SGM spatial density in this study. This is most likely due to the small size of the island, with the spatial heterogeneity of these elements being insufficient to affect millipede spatial density.

In this study, SGM densities were greater in the elevated rock covered areas, compared with the lower-lying non-rock covered areas. Millipedes are highly susceptible to desiccation and have evolved a variety of behavioural mechanisms to reduce water loss (Hopkin and Read 1992). Millipedes often temporally select areas with favourable temperature and humidity conditions to avoid unsuitable microclimates (Berġholz 2007). Here, individuals selected granite rock crevices in forest covered areas for

diurnal refuges, as microclimate conditions in these crevices were similar to nocturnal conditions on the forest floor. On Cousine, granite rocks form highly prominent and abundant features (Samways et al. 2010b), and therefore represent a readily available resource. Elsewhere, granite rocks have been shown to form important refuges for many ground-dwelling invertebrates, including millipedes (Ferreira et al. 2009).

Yet, granite rock crevices were not the only diurnal refuges used by the SGM. Individuals were seen under fallen logs and rotting wood debris. Such refuges would certainly provide suitable microclimate conditions for this species, as temperature and humidity conditions were approximately 2 ºC and 12 to 15 % RH lower and moister respectively than ambient conditions (Kelly and Samways 2003). Coarse woody debris, including logs, form important habitat elements for many soil and litter-dwelling invertebrate species (Ulyshen and Hanula 2009). However, log debris was widely spaced and in low abundance compared to granite rock cover on Cousine, resulting in millipedes favouring rock crevices.

Furthermore, the soil environment can be a potentially important habitat element for adult millipedes, with animals burrowing to avoid unfavourable microclimate conditions (Dangerfield and Chipfunde 1995). Additionally, millipedes have been known to include soil in their diet (Dangerfield 1993). However, the soil properties measured here had little impact on millipede spatial density, with SGM individuals rarely seen burrowing or feeding on soil (Lawrence and Samways 2003).

As little is known about the immature stages of the SGM, this study focused on adult millipede requirements. Like most spirostreptid millipedes (McMonigle 2005), the SGM lays eggs in the soil, with young millipedes (Mean length ± SD: 15.4 ± 2.3 mm; n = 10) spending a large proportion of time in the soil environment as opposed to on the surface (J. Lawrence, unpubl. data). This suggests that the soil environment may influence egg-laying behaviour and young millipede survival. However, the influence of the soil environment on SGM early stages is not known and would require further investigation.

Canopy cover in the restored forest was comparable with that in the natural forest on Cousine (Lawrence et al. 2012). A closed canopy forest is considered important for successful ground-dwelling invertebrate colonisation of restored forests (Nakamura et al. 2009). Here, low granite rock cover in the restored forest on Cousine was clearly a limiting habitat element. Key habitat elements can also be context specific. Surface microclimates can be inextricably linked to topography and vegetation structure (Kang et al. 2000), with a closed canopy forest significantly reducing diurnal microclimate conditions in crevices to suitable levels, compared with those in non-forest covered areas. This is clearly supported by the physical condition data, as the activity rating of individuals in non-forest covered crevices was lower compared to those in forest-covered crevices. Moreover, a closed canopy forest would provide abundant leaf litter for the SGM to feed on, as was shown by the increase in SGM foraging observations in the restored area following forest restoration practices (Lawrence et al. 2012).

Similar to butterfly requirements (Dennis 2010), a vegetation-based habitat view is insufficient for understanding the SGM's requirements, as its habitat needs extend beyond that of vegetation alone. Employing a resource and condition based habitat view would make it possible to predict a target invertebrate's response to management and successional changes resulting from restoration practices.

Ideally, key habitat requirements should be determined in a target invertebrate's source area (Samways et al. 2010a), as its minimum needs would be met there. However, identifying essential key habitat elements is time consuming and relies on a detailed autecological study of the target invertebrate's biology. Although I focussed on selected surface elements, other factors, not identified here, could potentially affect SGM colonisation of restored Seychelles forests (e.g. soil type and chemical composition; exposure to wind; restoration site age).

Closely linked with identifying essential habitat elements is an understanding of why these elements are important. Although granite rocks are key habitat elements for the SGM, their real value for this species is that they form suitable daytime refuges with favourable microclimate conditions. While the physical addition of granite rocks to the restored area is impractical, the use of surrogates (i.e. woody material etc.) is a possible management option (Stokland et al. 2012). As the restored forest matures, coarse woody debris would be expected to increase in abundance, depending on the management practices employed. However, the value of coarse woody debris as millipede refuges would still need to be quantified before this can be considered a suitable management option. Alternatively, selecting restoration sites that already have abundant rock cover would be the most practical way to increase SGM habitat through forest restoration practices.

If restoring habitat for target invertebrates is to be successful, we need to move from a primarily vegetation-based approach to a method that focuses on both biotic and abiotic resources that are essential for their survival. For habitat restoration planning and management, it is important to know exactly which resources and conditions are key habitat elements so as to optimise practical conservation action. Furthermore, taking into consideration the habitat requirements of selected target invertebrates could help in setting or re-directing restoration goals and thus ultimately enhance the overall conservation value of the project.

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Table 5.1 Summary of surface habitat elements, methods used and sample sizes (n)

Surface habitat elements	Methods	n
Edaphic properties		
Soil moisture	Horticulture soil moisture meter at 0.11 m depth [Note a,b] Scale: 1 (dry) – 10 (wet)	240
Soil pH	Horticulture pH meter at 0.11 m depth [Note a]	60
Soil depth	Penetrating depth of sharpened aluminium rod [Note b] (m)	240
Soil compaction	Humboldt soil penetrometer [Note b] ($kg.cm^{-2}$)	240
Litter material		
Wood debris	Counts of all wood debris contacts made with 10 m rope along transect ($total.m^{-1}$)	60
Leaf litter	Visual estimation of leaf litter covering quadrat (nearest 10%)	60
Toposcape		
Granite rock	Length of rock contacts made with 10 m tape measure along transect (nearest 5%)	60
Elevation	Oregon Scientific pressure altimeter (feet above sea level)	60

Note a: Mean Seychelles giant millipede burrow depth was 0.11 ± 0.04 m (n = 6) (unpubl. data).

Note b: Average of four readings taken per quadrat.

Table 5.2 Spearman Rank Correlation r_s values, *P* level, sample sizes (n) and figures, between *Sechelleptus seychellarum* density and surface habitat elements. Significant correlations in bold

Surface habitat elements	r_s value	*P* level	n	Figures
Edaphic properties				
Soil moisture	0.172	n.s.	240	Fig. 5.2a
Soil pH	-0.139	n.s.	60	Fig. 5.2b
Soil depth	0.051	n.s.	240	Fig. 5.2c
Soil compaction	-0.212	n.s.	240	Fig. 5.2d
Litter material				
Wood debris cover	0.031	n.s.	60	Fig. 5.2e
Leaf litter cover	-0.219	n.s.	60	Fig. 5.2f
Toposcape				
Granite rock cover	**0.855**	***P* < 0.001**	60	Fig. 5.2g
Elevation	**0.617**	***P* < 0.001**	60	Fig. 5.2h

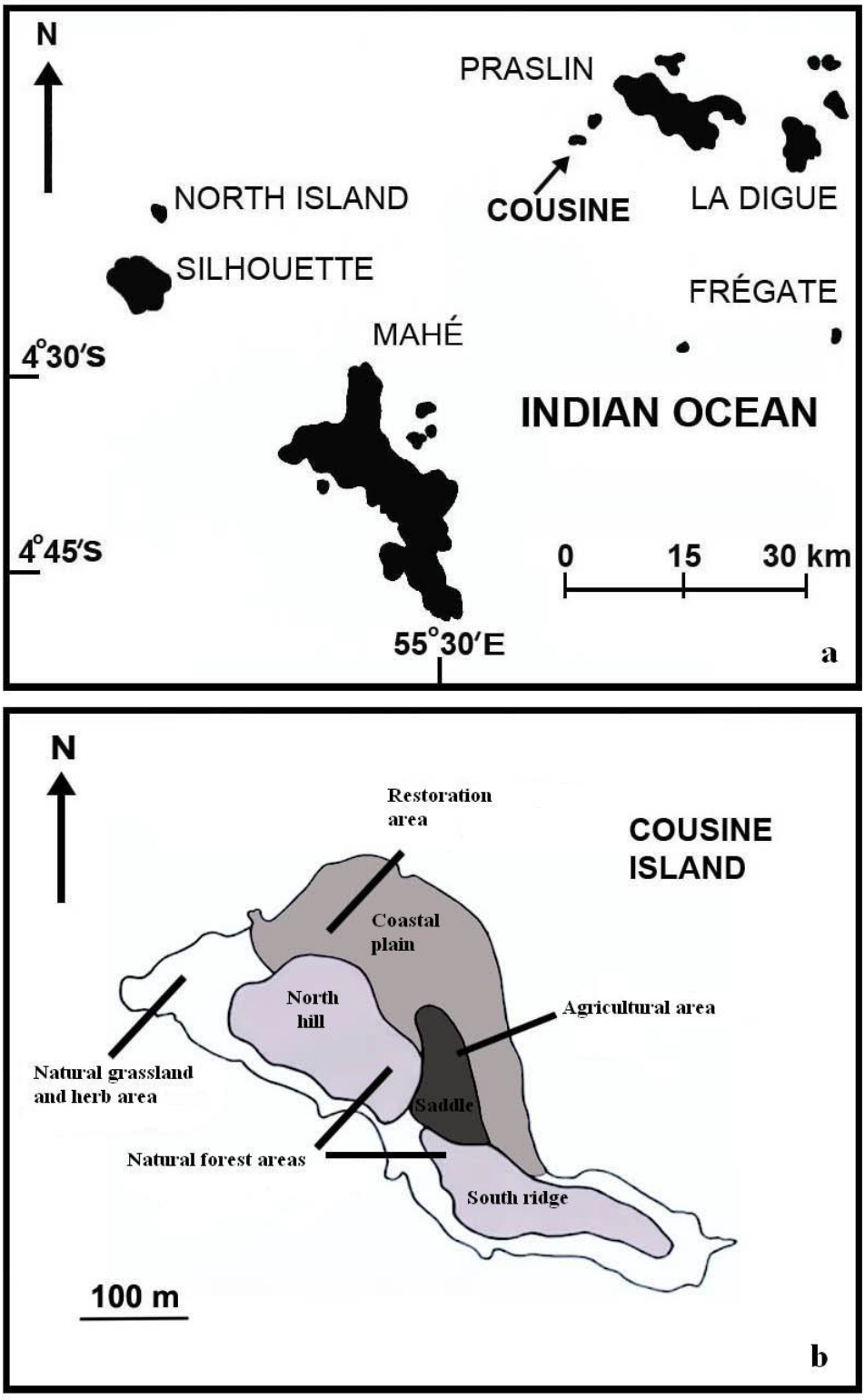

Fig. 5.1a Central group of Seychelles granitic islands, showing the position of Cousine Island, Seychelles; **b.** Simplified vegetation types and topography of Cousine Island, Seychelles

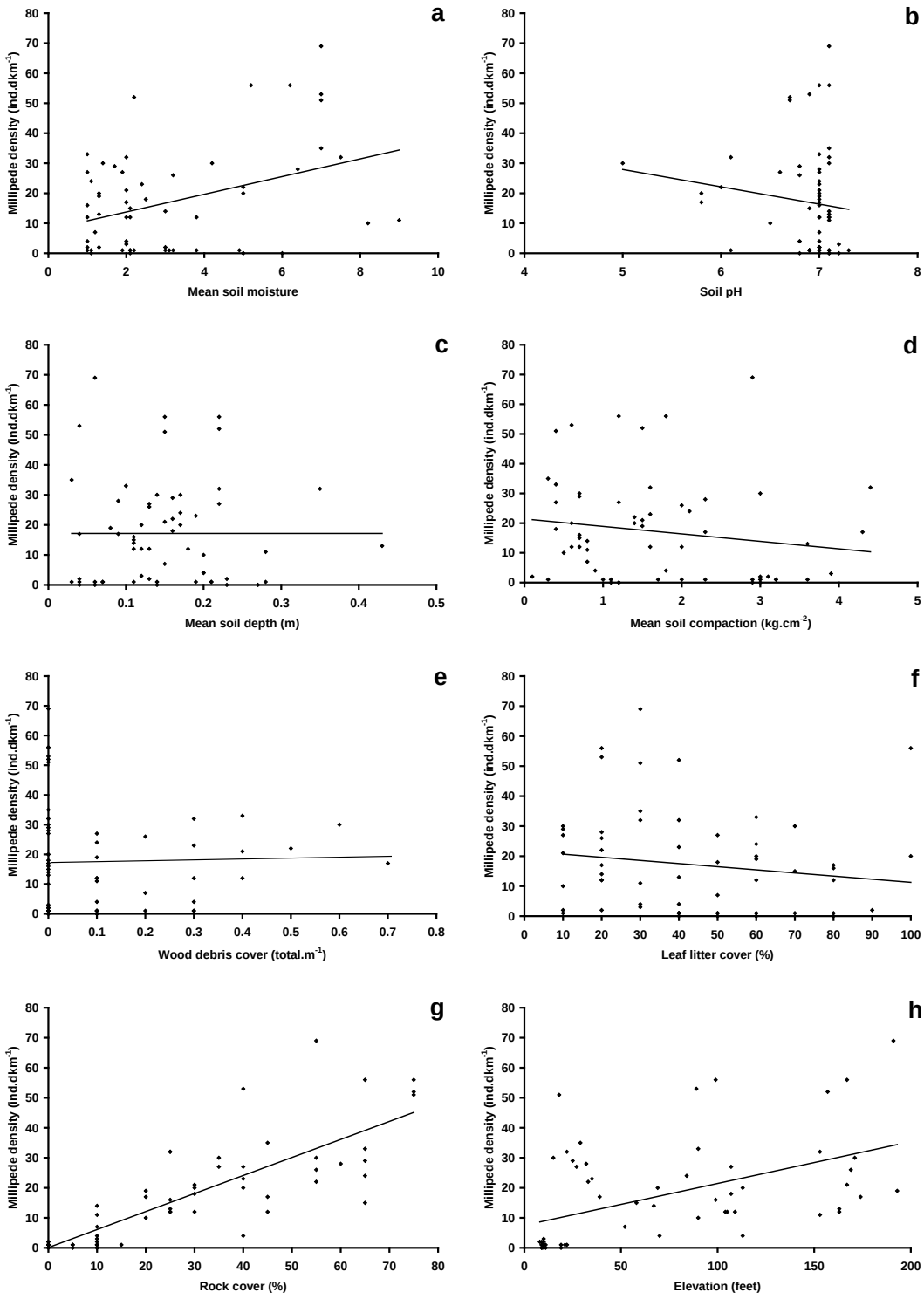

Fig. 5.2 Spearman Rank Correlations between millipede density (ind.dkm^{-1}) and **a.** mean soil moisture; **b.** soil pH; **c.** mean soil depth (m); **d.** mean soil compaction (kg.m^{-2}); **e.** wood debris cover (total.m^{-1}); **f.** leaf litter cover (%); **g.** rock cover (%); **h.** elevation (feet). NOTE: ind. = individuals; dkm = decametre (i.e. 1 m × 10 m)

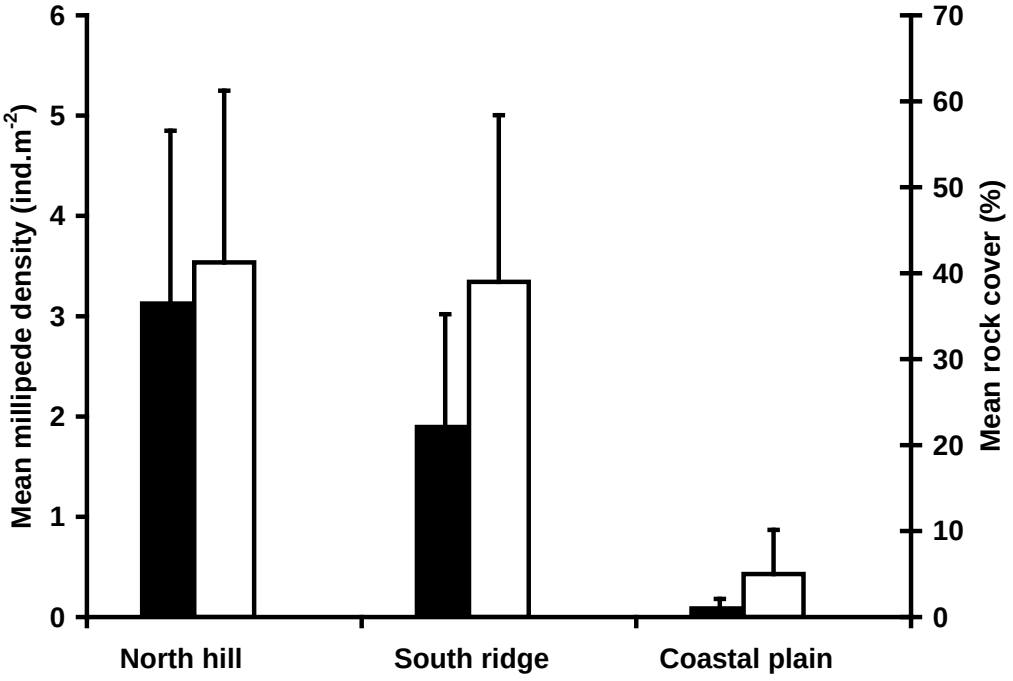

Fig. 5.3 Spatial relationship between *Sechelleptus seychellarum* and rock cover in the following forest covered areas on Cousine, Seychelles: North hill (Natural Forest; n = 20); South ridge (Natural Forest; n = 20); Coastal plain (Restored Forest; n = 20). *Black bar* mean millipede density ± SD (ind.m^{-2}); *White bar* mean percentage rock cover ± SD (%). NOTE: ind. = individuals

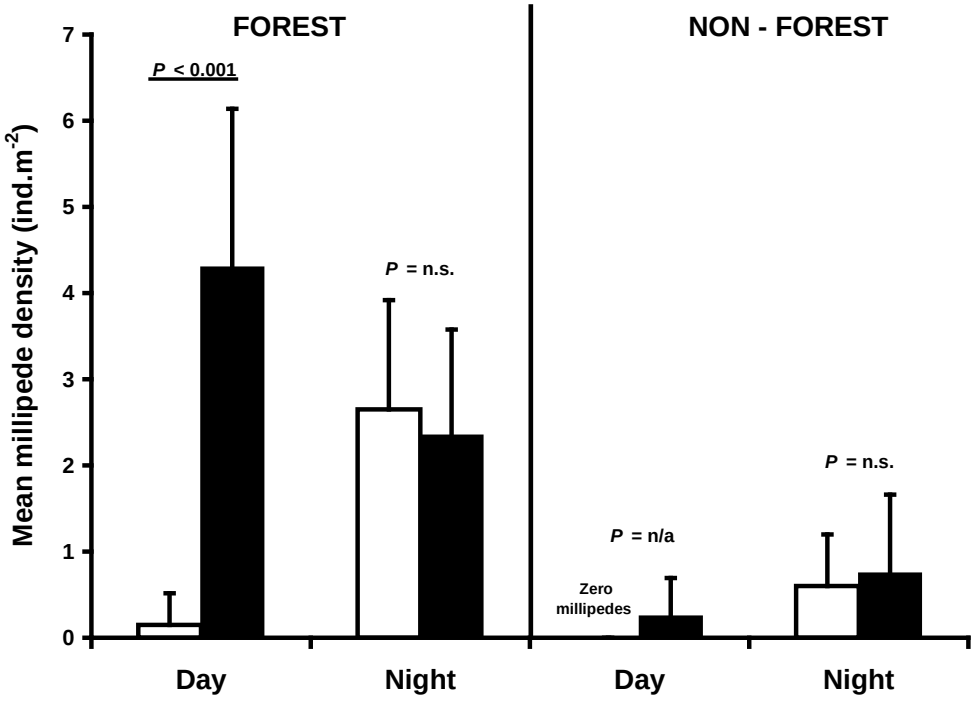

Fig. 5.4 Nocturnal and diurnal *Sechelleptus seychellarum* densities per 1 m^2 rocky/bare quadrat pairs in forest covered (n = 40) and non-forest covered (n = 40) areas on Cousine Island, Seychelles. *White bar* mean millipede density ± SD per bare quadrat (ind.m^{-2}); *Black bar* mean millipede density ± SD per rocky quadrat (ind.m^{-2}). Mann-Whitney U Test between bare and rocky quadrats provided, with significant *P* value underlined. NOTE: ind. = individuals; n.s. = not significant

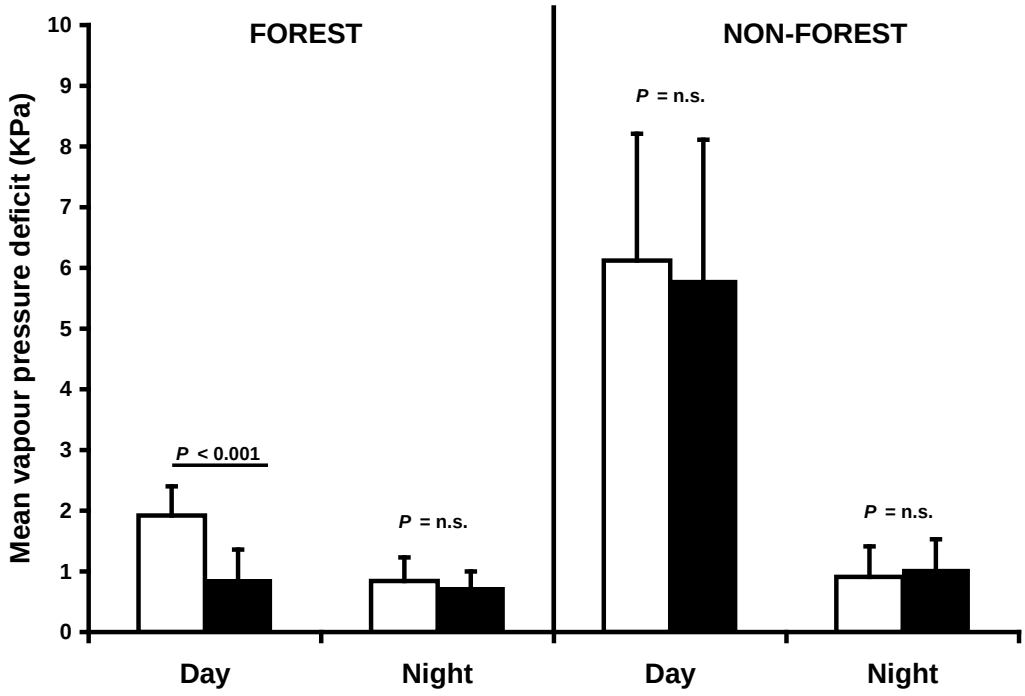

Fig. 5.5 Nocturnal and diurnal vapour pressure deficit (VPD) (KPa) in rock crevices/bare ground spot point pairs in forest covered (n = 40) and non-forest covered (n = 40) areas on Cousine Island, Seychelles. *White bar* mean VPD ± SD per bare ground spot point; *Black bar* mean VPD ± SD per rock crevice. Mann-Whitney U Test between bare ground spot points and rock crevices provided, with significant *P* value underlined. NOTE: n.s. = not significant

CHAPTER 6

Summary and conclusions

6.1. Introduction

The aim of this study was to contribute towards our understanding of how restoration practices, which have historically been based on broad generalised principles, can be directed or re-directed to assist in the conservation of threatened and functionally important target invertebrates. Soil macroinvertebrates (i.e. earthworms, millipedes and isopods) are recognised as integral components of terrestrial ecosystems (Coleman et al. 2004; Bardgett 200; Bardgett and Wardle 2010; Boyer and Wratten 2010), yet they have been neglected to a great extent in restoration practices (Snyder and Hendrix 2008). This particular study focussed on the autecological requirements of the Seychelles giant millipede (SGM), *Sechelleptus seychellarum*, in relation to the ongoing plant community restoration programme on Cousine Island, Seychelles. This species was chosen as it is a large, charismatic and threatened invertebrate that plays a keystone role in litter breakdown and nutrient dynamics. The restoration of the SGM's habitat is therefore not only about conserving a threatened species, but also about restoring an essential ecological process.

6.2. Chapter summaries

6.2.1. Significance of population dynamics

Species translocations can play an important role in the conservation and restoration of target species. This can be especially important for island species that often have small population sizes and are potentially limited by lack of suitable habitat. An understanding of a target species' population dynamics plays a significant role in translocating species to new habitats. For the SGM, population density not only fluctuates annually, with millipedes more abundant during the wet NW monsoon period, but also inter-annually. In Chapter 2, I recommend that for the SGM, potential translocations should take place in years when millipede surface densities are high and during the NW monsoon period. Furthermore, populations should aim to establish a female:male:juvenile ratio of ~ 3:1:1. While this study does not suggest that the SGM must be translocated to other islands for its continued survival, the data presented in this Chapter provide some population guidelines for such a conservation management approach.

6.2.2. Understanding a target species' response to specific threats

Understanding the key threats that a target species faces is essential for the conservation and restoration of that species. Without the removal of these key threats, such efforts will fail. For most invertebrate focussed studies, population density is generally used as a proxy for determining a species' response to a specific threat. In Chapter 3, I show the importance of taking into account behavioural ecology when assessing the impacts of habitat deterioration on a target species. For the SGM, coconut stands did not affect its population density, but clearly affected its foraging ecology, whereas bamboo affected both its population density and foraging ecology. Alien bamboo and coconut stands therefore pose a varied threat to the SGM, and their removal and replacement by indigenous forest species (e.g. *P. grandis* and *Ficus* sp.) should form part of an islands restoration programme.

6.2.3. Understanding a target species' response to plant community restoration practices

Understanding the response of target invertebrates to plant community restoration practices can be vital for the successful conservation of such species. In Chapter 4, I show that a species' response to such practice is not always clear-cut. While focussing on the population response is certainly more useful from a conservation perspective, understanding how restoration practices can influences a species' behaviour and physical condition can indicate that certain key resources may be limiting, thus assisting with understanding a target invertebrate's habitat requirements. In the time frame of this study, the SGM failed to successfully colonise the restored site in similar densities to that in the natural reference forest. Nevertheless, the forest restoration programme did benefit the SGM by providing more extensive foraging areas and improved conditions for it.

6.2.4. Understanding a target species' habitat requirements

Many vegetation-based restoration practices often fail to attract the desired fauna. This is because an invertebrate's habitat requirements often extend beyond that of vegetation. A purely vegetation-based approach to restoring habitat for fauna will result in a haphazard colonisation of such sites by animals. If restoring habitat for target invertebrates is to be successful, we need to move from a primarily vegetation-based approach to a method that focuses on both biotic and abiotic resources that are essential for their survival. Taking into consideration the habitat requirements of selected target invertebrates could help in setting or re-directing restoration goals and thus ultimately enhance the overall conservation value of such

practices. As demonstrated in Chapter 5, this was clearly the case for the SGM. While an indigenous closed-canopy forest is certainly an important facet of its habitat, granitic rock crevices in these forests were shown to provide essential day-time refuges for this species, by creating suitable micro-climate conditions. Selecting restoration sites that already have abundant rock cover would be the most practical way to increase SGM habitat through forest restoration practices.

6.3. Habitat restoration verse biotope restoration

Firstly, I would like to briefly recap on the difference between a biotope and a habitat as outlined in Chapter 1, as understanding this distinction is essential for this discussion. A biotope is a region (an area for example: woodland, tropical forest, heath, cliff) that is distinguished by particular environmental conditions (Webb 1993) and will therefore tend to contain a characteristic assemblage of species (Calow 1999). Historically, most restoration projects have been vegetation-based (Young 2000) and therefore only restore a specific biotope. Habitat is a species-specific concept (Hall et al. 1997) and is far better understood in terms of a species' resource requirements (Dennis 2010).

Invertebrates generally play a role in the assessment of the success of restoration practices. Very few studies have focussed specifically on restoring habitat for threatened invertebrates, making comparison of the results in this dissertation with other studies difficult. Most studies that have looked at restoring habitat for invertebrates have been broad-based and biotope-focussed (e.g. generally vegetation-focussed), and have often resulted in restoring a limited assemblage of the species that occur in the area (e.g. Waltz and Covington 2004).

Of the few studies that have focussed on the habitat requirements of threatened invertebrates, most have focussed on butterflies and have been principally vegetation-based (Schultz 2001; New 2009; New 2011). The results presented in this dissertation clearly indicate that habitat restoration goes beyond that of a biotope for some invertebrate species. While vegetation restoration was clearly an essential part of the SGM's habitat requirements (i.e. removal of alien vegetation; restored forest provided food), granitic rocks formed essential day-time refuges for the SGM by providing suitable micro-climate conditions for this species. Despite the influences of microclimates on invertebrate habitat selection and micro-distributions being well known (Unwin and Corbet 1991), I know of only two other studies that have highlighted the importance of micro-climate in restoring habitat for invertebrates, and both have focussed, again, on butterflies (Weiss and Murphy 1990; Meyer and Sisk 2001).

However, there are numerous studies that have shown that many threatened invertebrates have habitat requirements that go beyond vegetation. For example, the highly threatened (possibly extinct) Franklin's bumblebee, *Bombus franklini* (Frison) nests in rodent burrows (Thorp et al. 2010). In another example, Wallace's bee, *Chalicodoma pluto* (Smith), which was thought extinct until rediscovered in 1981 (New 2012), shares an obligatory association with *Microcerotermes* termites (Messer 1984). In one final

example, the threatened Banks Peninsula tree weta, *Hemideina ricta* Hutton, lives in holes, cracks and crevices of mature trees and rock stacks (Townsend et al. 1997). Clearly, a purely vegetation-based view to restoring habitat for these invertebrates would potentially fail, and the specialised requirements of these invertebrates need to be taken into account.

This dissertation clearly highlights that restoration ecology as it stands at present lacks specific useable definitions that can assist in setting achievable restoration goals. Restoration ecology is defined by the Society for Ecological Restoration as "the process of assisting the recovery of an ecosystem that has been degraded, damaged or destroyed'. This definition is very broad and applies specifically to ecosystems. This is fine for biotope-based restoration projects but can be misleading for directing habitat restoration. I suggest that restoration ecology should clearly differentiate between biotope-based and habitat-based restoration, as both would have specific goals and approaches to achieving their respective aims. As restoring sites for invertebrate conservation is intimately associated with the establishment of the plantscape in which invertebrates live (Samways 1994), the restoring of an invertebrates preferred vegetation biotope is obviously an essential aspect. However, as this dissertation demonstrates, for habitat restoration to be successful, it would have go beyond a biotope-based approach and focus on the specific resource requirements of target species (e.g. restoring suitable micro-climate conditions for target species).

6.4. Conclusions and future research

In conclusion, the objectives of this project were met. Practical recommendations have been made that can be applied to future Seychelles restoration programmes that aim to take into account the needs of the SGM. With approximately 45 % of Seychelles under protection (Tingay 2010), and several of the islands undergoing some form of restoration (e.g. Cousine, Cousin, Aride and Frégate islands) (Shah 2001; 2006; Henri et al. 2004; Samways et al. 2010), the short-term future of the SGM would appear to be secure, although its long-term survival is unclear. Not fully understanding the cause of the recent large decrease in SGM numbers on the low-lying islands is still a cause for concern. This, in combination with its potential vulnerability to rat predation and human traffic (IUCN 2011) adds further concern to the long-term survival of this species, as the extinction of species' is often caused by a combination of factors (Brook et al. 2008). Furthermore, there are currently no management (in particular monitoring) programmes in place which would give advanced warning of any potential future decreases in millipede numbers. As a result, I would recommend continued monitoring of this species, at least on an annual basis. The SGM is easily observed, and such a monitoring programme could effortlessly be included in the conservation programmes on the islands of Cousine, Cousin, Aride and Frégate.

Despite this project focussing on several aspects of the autecology of the SGM, with specific reference to restoration practices, there is still much to be learnt about the conservation and restoration of this species. Firstly, the life history of the SGM needs to be described. This would certainly help with

identifying and understanding the habitat requirements of the early life stages of this species. In general, millipedes are long lived, with cryptic and complex life histories. Secondly, the SGM does show slight morphological variation amongst island populations. Genetic work would be essential for determining any possibly taxonomic differences. This has important implications for any potential translocation programmes. Thirdly, trying to gain an understanding of the causes of the large fluctuations in millipede numbers is important for the long-term monitoring of this species. Finally, the true test of the results presented in the project, would be to translocate millipedes to a suitable restored forest (i.e. one that has abundant rock cover on the forest floor). Possibly, in the future such a project will be carried out.

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